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1983

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BATCH FECUNDITY AND SPAWNING FREQUENCY OF VARIOUS ANCHOVY (Genus: *Engraulis*) POPULATIONS FROM UPWELLING AREAS AND THEIR USE FOR SPAWNING BIOMASS ESTIMATES*

by

J. Alheit,[1] B. Alegre,[2] V.H. Alarcōn,[2]
and B. Macewicz[3]

[1] Programa Cooperativo Peruano-Alemān de Investigaciōn
Pesquera (PROCOPA), IMARPE, Apartado 22, Callao, Perū

[2] Instituto del Mar del Perū, Apartado 22, Callao, Perū

[3] Southwest Fisheries Center, P.O. Box 271, La Jolla,
CA 92038, U.S.A.

* Publication No. 7 of PROCOPA

Resumen

Recientemente se han revelado varias características esenciales de la biología reproductiva de la anchoveta peruana (*Engraulis ringens*) y ahora pueden ser comparadas con aquellas de la anchoveta del norte (*E. mordax*). Así como la anchoveta del norte, la anchoveta de sistema de afloramientos de Perú desova en forma parcial, depositando varias series de huevos a lo largo del año. Ahora se dispone de datos de series de tiempo sobre la fecundidad parcial de varias sub-poblaciones de ambas especies. La variabilidad de la fecundidad parcial es alta dentro de cada año y de un año a otro. En ambas especies, la fecundidad parcial aumenta a medida que aumenta la latitud. Fuera de las épocas principales de desove (Agosto-Septiembre y Enero) la fecundidad parcial de la anchoveta peruana disminuye. Durante El Niño de 1976, la fecundidad parcial de *E. ringes* disminuyó considerablemente. Esto se atribuye a las condiciones desfavorables de alimentación. La fecundidad parcial de *E. capensis* frente al sudoeste de Africa se encuentra dentro del rango de los valores de las otras dos especies. La frecuencia del desove fue determinada por exámenes histólogicos de los ovarios para observar la incidencia de folículos post-ovulatorios. La fracción de hembras maduras que desovan por día fue de 16% en 1961 frente a Perú y 14.5% en 1980 frente a California. Todos los parámetros reproductivos investigados son muy similares en ambas especies, indicando una relación filogénetica estrecha. La importancia de determinar la fecundidad parcial y la frecuencia del desove se basa en su uso para "el método de la producción de huevos" que fue desarrollado recientemente para estimar la biomasa desovante de anchoveta. Este método ha sido aplicado con suceso en los stocks de anchovetas frente a California y Perú. Se discuten los resultados, ventajas y futuras aplicaciones de este método para otras especies de peces pelágicos que forman cardúmenes tales como sardinas.

INTRODUCTION

Recently, a new method, the 'Egg Production Method', was developed by the Southwest Fisheries Center, California, to estimate the spawning biomass of anchovies (Parker, 1980; Stauffer and Picquelle, 1980). This method requires the determination of reproductive parameters like batch fecundity and spawning frequency, i.e. the fraction of mature females spawning per day.

The determination of batch fecundity and spawning frequency for multiple spawning pelagic fish, like the anchovy, posed several problems which were solved by Hunter and Goldberg (1980). In traditional methods, size - frequency diagrams of oocytes were established and it was assumed that fecundity could be determined by counting the number of all oocytes contained in the most advanced mode. Hunter and Goldberg (1980) discussed the problems involved in this method. Instead, they determined the batch fecundity by counting the number of hydrated oocytes in the ovaries. This method takes much less time and yields a higher precision than traditional methods. For the determination of the spawning frequency, Hunter and Goldberg (1980) used the incidence of postovulatory follicles in anchovies. They were able to age postovulatory follicles and to determine the day when a particular female had spawned. All these studies were carried out on the northern anchovy (*Engraulis mordax*). Recently, the same methods were applied successfully, to the Peruvian anchovy (*E. ringens*) (Alheit el al., in prep.; Santander et al., in prep.).

Time series are available now on the batch fecundity of the Peruvian and the northern anchovy. The data were partly gained from previous studies using traditional methods (MacGregor, 1968; Laroche and Richardson, 1980) and from samples collected in Peru during the seventies which were processed recently.

The objectives of this study are (1) to compare the time series on batch fecundity of the two anchovy species, (2) to compare for both species the data on batch fecundity and spawning frequency gained by the new methods, and (3) to discuss their use for estimates of spawning biomass of multiple spawning pelagic fish.

This study was a cooperative effort of the Southwest Fisheries Center, California, the Instituto del Mar del Peru and the Peruvian-German Fisheries Research Project (PROCOPA) which is financed by the German Agency of Technical Cooperation (GTZ).

METHODS

The batch fecundity of the Peruvian anchovy samples collected in the seventies was determined by macerating the connective tissue of the ovaries in Gilson's fluid (Simpson, 1951), a process which releases the oocytes. The size of the oocytes was measured and the number of oocytes in the most advanced mode was determined by means of probability paper (Cassie, 1954). The recent batch fecundity data for the Peruvian and northern anchovy were gained by using hydrated oocytes (Hunter and Goldberg, 1980). The methods used for determining the batch fecundity of other anchovy populations presented here are described in MacGregor (1968) for the northern anchovy in 1951-60, in Laroche and Richardson (1980) for the northern population of the northern anchovy and in LeClus (1979) for the anchovy off South West Africa (*E. capensis*). The spawning frequency was determined according to the methods described by Hunter and Goldberg (1980), Stauffer and Picquelle (1980) and Alheit et al. (in prep.).

Table 1: Mean number of oocytes per gram ovary, mean number of oocytes per gram female and geometric mean regression (Ricker, 1973) of eggs per spawn (= batch fecundity) on gonad-free female wet weight.

Nr.	Species	Sub-population	Year	Month	Sample Size	Size Range of fish (gonad-free weight in g)	Mean Nr Oocytes per g female	S.D.	Mean Nr. Oocytes per g Ovary	S.D.	r	Slope	Y-intercept
1	E. ringens	central	1970	Jan	19	15.2 - 40.0	7 123	± 2719	375	± 147	.685	1 048	-16 627
2	" "	"	1973	Sep	26	15.1 - 38.7	5 998	± 2728	410	± 172	.564	746	- 8 527
3	" "	"	1974	Jan	8	22.8 - 43.2	9 231	± 1938	489	± 133	.554	847	-13 125
4	" "	"	"	Feb	8	32.2 - 44.2	6 011	± 999	326	± 91	.126	667	-13 506
5	" "	"	"	Aug	12	17.7 - 41.3	7 067	± 2049	484	± 157	.717	1 517	-31 194
6	" "	"	"	Sep	9	21.0 - 48.4	8 233	± 1577	410	± 142	.692	705	- 8 814
7	" "	"	"	Oct	18	16.3 - 54.5	6 607	± 2295	268	± 110	.799	558	- 8 804
8	" "	"	1976	Aug	32	6.8 - 34.5	11 606	± 5447	415	± 143	.813	424	- 227
9	" "	"	"	"	11	15.0 - 34.5	7 686	± 1800	414	± 149	.509	360	1 257
10	" "	southern	1973	Sep	19	14.1 - 21.7	7 205	± 3125	395	± 122	.614	1 352	-17 490
11	" "	"	1974	Aug	23	9.0 - 41.3	6 432	± 2351	446	± 175	.831	1 087	-13 545
12	" "	northern + central	1981	Aug/ Sep	437	15.0 - 38.0	*)		580	± 139	.806	981	-10 279
13	E. ringens	central	1981	Aug/ Sep	254	15.0 - 38.0	*)		637	± 134	.769	1 213	-14 745
14	" "	northern	"	Aug/ Sep	183	15.0 - 38.0	*)		502	± 103	.883	824	- 7 655
15	E. mordax[1]	central	1951-1960		19	9.3 - 32.1	12 253	± 2737	606	± 151	.795	670	- 1 247
16	" "	"	1978		23	9.3 - 31.9	*)		389	± 141	.511	528	- 2 790
17	" "	"	1979		44	9.3 - 28.1	*)		438	± 150	.784	881	- 7 917
18	" "	"	1980		33	17.11+)	*)		444	± 80	.903	624	- 2 933
19	" "	"	1981		127	14.75+)	*)		601	± 180	.873	872	- 3 711
20	" "	"	1982		109	16.54+)	*)		606	± 151	.724	852	- 4 061
21	" "	northern[2]	1977		17	14.4 - 31.3	7 137	± 3997	869	± 213	.860	1 494	-12 015
22	E.capensis		1977		14	17.5 - 24.3	4 491	± 851	644	± 153	.451	1 542	-18 657

1) From MacGregor (1968) 2) From LaRoche and Richardson (1980) 3) From LeClus (1979)
*) Parameter not calculated as hydrated oocytes were used
+) Average weight

RESULTS

Time series on fecundity of Peruvian anchovy. 14 different data sets on fecundity of the Peruvian anchovy are available (Table 1). They originate from different years, months and areas. There are no trends recognizable for the mean number of oocytes per gram female, however, some interesting features can be pointed out. Only one data set, January 1970, was collected before the crash of the Peruvian anchovy in 1972. This value is relatively, but not particularly low. The data set from August 1976 was collected during an 'El Niño' year. The collection includes many very small mature females between 7 and 15 g. To make this data more comparable, another data set comprising only the larger specimens (11 fish) is presented separately. The values from August 1976 lie just within the range of the other data sets. There are two data sets from the south, but they are not outliers. The only remarkable feature is the difference between the relatively low values from the seventies and the high values from 1981. This difference is probably not caused by the use of different methods. In 1981, two data sets were taken, one from the central region and one from the northern region. The one from the central region is with 637 eggs per gram female; much higher than the 499 eggs per gram female from the northern region. This might not necessarily be a regional difference, as the northern samples were, on average, collected two weeks later than the central samples. It could be that the value for the number of eggs per gram female is very flexible and can change very fast towards the end of the spawning season. In general, one can observe a decrease of the mean number of eggs per gram female after the main spawning periods in August/September and January, e.g. in 1974 and 1981. The number of oocytes per gram ovary, does not show any trend. Only the value for the large data set from August 1976 lies outside of the range of the other values. However, this high value is caused, solely, by the high number of very small mature females. The mean number of oocytes per gram ovary is not given for 1981, as this value changes during the process of hydration.

The relationship between batch fecundity and female weight (ovary-free) was investigated further by using the geometric mean regression (Ricker, 1973) Whereas all other data from the Peruvian anchovy have a relatively high Y - intercept, only the data from August 1976 have a positive and a relatively low negative value (Table 1). Differences between the 14 data sets become more obvious from the regression lines in Figures 1-3. They are presented in three different groups whereby the whole data set from August 1981 serves as a reference line. Group 1 includes all the data collected during the yearly peak spawning periods in August/September and January (Figure 1). These regression lines are not too different from each other. The second group comprises the 'El Niño' data from August 1976 and data sets collected at February 1974 and October 1974, outside of the yearly main spawning periods (Figure 2). These data sets have in common a relatively low batch fecundity for females larger than 30 g. The third group demonstrates regional differences. Obviously the fecundity values from the southern Peruvian anchovy stock are higher than in the central and northern stock. Although the data sets were taken in

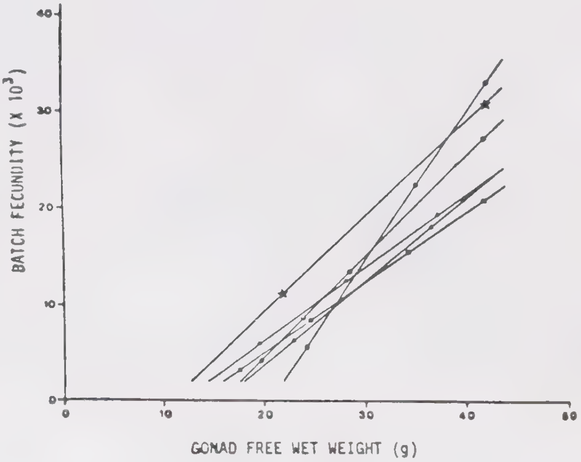

Fig. 1. Batch fecundity of *E. ringens* populations. Geometric mean regression of number of eggs per spawn on gonad-free female wet weight.

★ = Lots 12 - 14 ○ = Lot 1
● = Lot 11 ▲ = Lot 2
△ = Lot 3 ■ = Lot 6

different years, they indicate, that the batch fecundity increases with increasing latitude (Figure 3).

Comparison of fecundity of different anchovy species. Batch fecundity data are available for the Peruvian anchovy, the northern anchovy and the anchovy from South West Africa. The values for the mean number of oocytes per gram female from the northern anchovy and the anchovy off South West Africa lie within the range of the Peruvian data (Table 1). The only exception is the high value for the northern population of the northern anchovy. From 1978 to 1982 the values of the central population of the northern anchovy increased steadily from 389 to 606 eggs per gram female weight.

The regression lines of the central population of the northern anchovy are relatively uniform (Figure 4). However, the regression line of the northern population is very distinct and demonstrates that females with more than 15 g weight have a much higher batch fecundity than in the central population. Again, as in Peru, the batch fecundity of anchovy populations increases with increasing latitude.

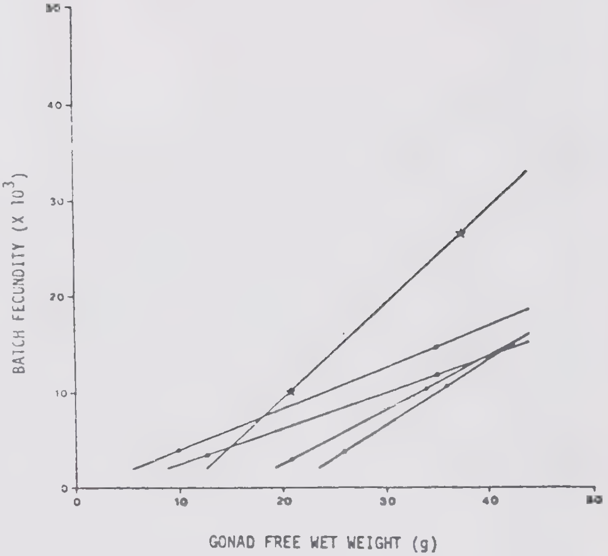

Fig. 2. Batch fecundity of *E. ringens* populations. Geometric mean regression of number of eggs per spawn on gonad-free female wet weight.

★ = Lots 12 - 14
● = Lot 8
▲ = Lot 7
○ = Lot 8 (only females >12 g).
△ = Lot 4

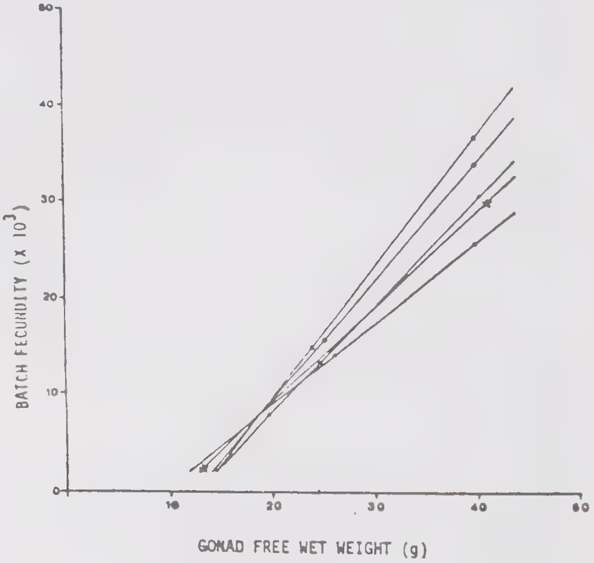

Fig. 3. Batch fecundity of *E. ringens* populations. Geometric mean regression of number of eggs per spawn on gonad-free female wet weight.

★ = Lots 12 - 14
● = Lot 10
▲ = Lot 11
○ = Lot 13
△ = Lot 4

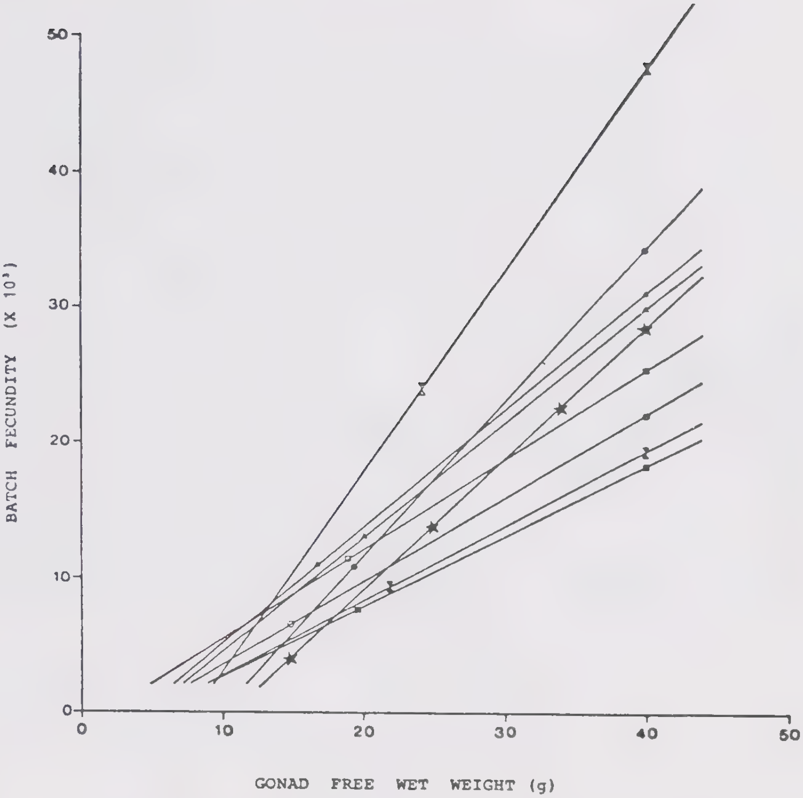

Fig. 4. Comparison of Different Species. Batch fecundity of anchovy populations. Geometric mean regression of number of eggs per spawn on gonad-free female wet weight.

★ = Lots 12 - 14 *E. ringens*
● = Lot 17 *E. mordax*
▲ = Lot 20 *E. mordax*
○ = Lot 18 *E. mordax*
⧗ = Lot 22 *E. capensis*

⧖ = Lot 21 *E. mordax*
△ = Lot 19 *E. mordax*
□ = Lot 15 *E. mordax*
■ = Lot 16 *E. mordax*, 1978, central population

Spawning frequency. The fraction of mature females spawning per day was determined for the Peruvian anchovy in August/September 1981. As a purse seiner was used to collect the adult anchovies, fish samples could be obtained at any time of the day and two data sets were established, one giving the fraction of females which spawned one day before being collected and the other one giving the fraction of females which had spawned two days before being sampled. These two spawning fractions were 17.26% and 14.81%, respectively (Alheit el al., in prep.).

The agreement of these two data sets demonstrates the validity of the method introduced by Hunter and Goldberg (1980). The spawning frequency determined for the Peruvian anchovy by combining these two data sets was 16.04%. That means every day during August/September 1981, on average, 16.04% of the mature females were spawning, or in other words, a female of the central and northern Peruvian stock spawned, on average, every 6.2 days a new batch of eggs. The spawning frequency recorded for the northern anchovy in 1981 was 14.5% (Stauffer and Picquelle, 1980) a value very similar to that one of the Peruvian anchovy.

Use of data on reproductive biology for estimates of spawning biomass. Batch fecundity and spawning frequency are two of the five parameters used for determining the spawning biomass of anchovies by means of the 'Egg Production Method' (Parker, 1980; Stauffer and Picquelle, 1980). So far, this method has been applied in California and Peru. The results of the Californian survey from 1980 (Stauffer and Picquelle, 1980) and from the Peruvian survey from 1981 (Santander et al., in prep.) are listed in Table 2.

Table 2: Results of spawning biomass estimates gained by application of 'Egg Production Method' in Peru 1981 and California 1980. Parameter estimates ($\hat{x}$) and estimates of spawning biomass with associated coefficient of variation ($CV_{\hat{x}}$). The data for Peru comes from Santander et al. (in prep.) and for California from Stauffer and Picquelle (1980).

	Peru 1981		California 1980	
	$\hat{x}$	$CV_{\hat{x}}$	$\hat{x}$	$CV_{\hat{x}}$
Daily egg production in survey area	6.985.10^3	0.2586	(10.50)*	0.103
Average female weight (g)	25.84	0.0259	17.50	0.0547
Fraction of females	0.564	0.0459	0.476	0.120
Batch fecundity (eggs/female)	15 401	0.0427	7 788	0.0749
Spawning frequency	0.160	0.0588	0.145	0.125
Spawning biomass (million tons)	1.295	0.2739	0.859	0.225

* This value is the number of eggs per ton.

DISCUSSION

The comparison of the batch fecundity data of different anchovy populations demonstrates clearly the high plasticity in batch fecundity of anchovies. There is a high variability in batch fecundity within years and between years as the Peruvian and Californian data show. One can only speculate about what causes this variability. Sufficient quantities of the right food are probably a very important condition for a fish to build up a high batch fecundity as argued by Bagenal (1978) and Wootton (1979). This might be indicated by the low fecundity values during the 'El Niño' year 1976 when feeding conditions were unfavourable for the Peruvian anchovy.

Tsukayama and Alvarez (1980) reported that during the 'El Niño' 1976 growth of the Peruvian anchovy was retarded and that the mean size of mature females was considerably less than in normal years. They suggested that the high proportion of small females would reduce the fecundity of the whole population. This hypothesis is confirmed by the data presented here. Population fecundity in 1976 was further reduced by the much lowered fecundity values of the larger females in comparison to other years (Figure 2). This lowered population fecundity is caused by the combined effect of a high proportion of small females and of large females having a lower batch fecundity than in normal years and certainly exerted a negative influence on subsequent recruitment.

The importance of the determination of batch fecundity and spawning frequency is based on their applications in the 'Egg Production Method' to estimate the spawning biomass of anchovies. The main advantages of the 'Egg Production Method' are its high precision and that it needs relatively little ship time. It consists of 5 biological parameters and error estimates can be determined for each of them (Table 2). To date, it has been applied four times in the Californian upwelling system (1980-1983) and once in Peru (1981).

Up to now, it was applied only to anchovies. However, it is suitable for other multiple spawning pelagic fish species, too. Recently, postovulatory follicles have been identified and aged for the Peruvian sardine (*Sardinops sagax sagax*) (Alarcon et al., in prep.), a vital step towards the application of the 'Egg Production Method' for sardines.

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25. CHAETOGNATHA

ANGELES ALVARIÑO

I. INTRODUCTION

The Chaetognatha are a group of enterocoelous, slender, transparent to translucent bilaterally symmetrical animals (Alvariño, 1963, 1965, 1967, 1969, for bibliography). The phylum includes only six genera, *Spadella* (benthic), and the pelagic *Eukrohnia*, *Krohnitta*, *Pterosagitta*, *Heterokrohnia*, and *Sagitta*. The benthic genus, *Spadella* comprises 12, *Eukrohnia* 5, *Krohnitta* 3, *Pterosagitta* 1 and *Heterokrohnia* 3 species; the genus *Sagitta* (with more than 40 species) includes most of the known species of Chaetognatha. The genus *Sagitta* appears to be the most successful and most highly evolved of the group; species of this genus inhabit the greatest variety of oceanic environments and bathymetric levels. The adult Chaetognatha of various species range in length from < 3 mm to > 100 mm. The body is divided into three morphologically well-differentiated regions, head, trunk, and tail, by transverse septa, and there is no communication across the trunk and tail septum (Fig. 1).

The Chaetognatha are hermaphroditic, but the female and male gonads are separated spatially in the body, and further, their maturity is separated temporally. The ovaries are in the trunk, together with the digestive tract, and the testes are in the tail, together with the seminal vesicles.

The reproduction of Chaetognatha has been discussed by several authors, mainly Grassi (1883), Ghirardelli (1968), Reeve (1970), and others. However, misconceptions in the description and interpretation of some aspects of the reproductive process persist in the literature. There is need for an anatomical study, and for relevant physiological interpretations based on morphology as well as behaviour. This review on the biology of reproduction is based on the anatomy of the reproductive organs and their function. The chaetognaths are difficult to maintain in the laboratory; experimental information is therefore scanty. The results should be considered within certain limitations: the behaviour of the animals in the laboratory would not accurately represent their normal life in the oceans. There is need for experimentation and more observations to understand their physiology and responses to changes in the environment, life cycle, and feeding conditions.

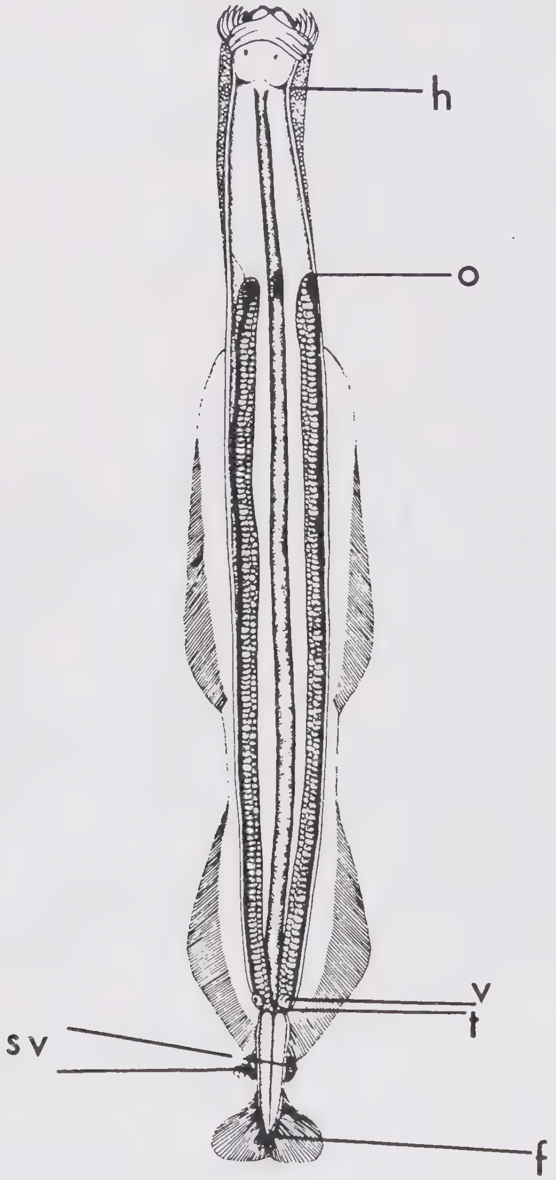

Fig. 1. *Sagitta scrippsae* (dorsal view) showing the disposition of female gonads in the trunk, and of the testes and seminal vesicles in the tail. Trunk, from h to t; ovaries, o to v; tail, t to f; sv, seminal vesicles

II. FEMALE REPRODUCTIVE SYSTEM

The first description of the morphology of the female reproductive apparatus in chaetognaths was given by Grassi (1883). Earlier observations by Butschli (1873), Hertwig (1880), and Grassi (1881) are only short notes. The female reproductive system (Fig. 1) is located totally in the trunk cavity and is separated from the male reproductive system by the transverse septum. The ovaries are elongated tubes, round in cross-section, lying at the posterior part of the trunk. They are attached to the body wall by a thin mesentery continuous with the lining of the trunk cavity in the region of the lateral line (Burfield, 1927; Alvariño, 1963, 1967); another fibrous ligament connects the posterior end of the ovary to the transverse septum near the anus. I have observed that the final extension of the fibrous mesentery reaches slightly further than the maximum extent of the full mature ovary.

Each ovary has, on its side facing the body wall, a seminal receptacle, which is in the form of a tube or thin canal running along the whole length of the ovary, and opening at its lowest end into the vaginal region. The sperm are stored in this receptacle after copulation. There is no direct communication between the ovary proper (zone occupied by the ova) and the seminal receptacle. Krohn (1853), and Leuckart and Pagenstecher (1858) had described the receptacle as a sperm pouch (*samentasche*). Keferstein (1862) considered it an oviduct, Wilms (1844) an excretory duct, and Huxley (1852), a ciliated canal. Grassi (1881) indicated that the 'spermduct' lumen varied in size with the quantity of spermatozoa contained, and that the walls were formed by single layer of cells. Stevens (1910) and Elpatiewsky (1913) described two layers of cells, the inner one a syncytium.

The seminal receptacle when full, forms an ampulla at the upper closed end. The masses of spermatozoa within the seminal receptacle are in a state of continuous movement, depending on the amount of spermatozoa stored therein. The seminal receptacle turns posteriorly at right angles into the vaginal cavity; the latter opens out through the external genital papilla. The walls of the vagina have two epithelial layers, an inner one formed of tall cylindrical cells with large vesicular nuclei and an outer one formed of thin, flat cells with elongated nuclei. The genital papilla is formed of glandular cells arranged in small cupula. Several elongated and fusiform elements make a sphincter that serves to close the orifice of the seminal receptacle. Both the ovary and seminal receptacle are covered by a thin endothelium.

The ovary, when mature, is full of linear rows of oocytes, attached to the lining of the ovary. All oocytes in the ovary are usually at the same stage of development, but not in *Sagitta bipunctata*. In animals full of ripe ova, the intestine may be displaced to one side by the bulky ovaries. The degree of maximum forward extension of the ovaries in the trunk cavity varies considerably with species. For instance, the ovary of *S. hispida* may extend up to the region of the ventral ganglion, and in *S. ferox* and *S. septata*, to the neck, while the mature ovaries of *S. enflata* occupy only a small portion of the total trunk length.

The penetration of the spermatozoa into the ova does not occur, as stated by several authors, while the ova are still in the ovary. The ova in the ovary of chaetognaths are not embryonated eggs, but only mature ova. If the ova were to be fertilized while still within the ovary, the development of the zygote would immediately follow, but this does not occur. I have observed and determined that the ova in the ovary are not zygotes. Therefore, it appears that fertilization of the ova takes place at the time of extrusion of the ova into the vaginal cavity, when the sperm are also released into that cavity from the seminal receptacle.

A. The Ovaries

The ovaries are two tubes situated right and left and opening to the vaginal cavity, and to the outside by the genital papillae, the latter located dorsal to the insertion of the lateral fins. Genital papillae and fins have respectively a dorsal and ventral position related to the lateral line of the body of the chaetognaths. In this manner, the opening is ventrally protected by the fins. The length the ovaries attain in fully mature individuals, varies with species, a characteristic used in diagnosing the species. The ovaries of various species of Chaetognatha have been described by Alvariño (1963, 1967, 1969), and only a summary is given here. The extension and length of the ovaries are related to other anatomical structures of the animal, such as anterior and posterior ends of the anterior or posterior fins, the ventral ganglion, and the neck region. Data on ovary characteristics for most species of chaetognaths are presented in Table. 1. Ovaries in *Eukrohnia bathypelagica* fill the body cavity and extend up to one-third the distance from ventral ganglion to tail septum, and appear to accumulate fatty tissue. The ovaries of immature specimens are coiled in an unusual way, but the coiling disappears progressively with maturity. In *E. fowleri*, ovaries are short and thick, and the seminal receptacle is large. In *E. hamata*, ovaries extend halfway between the caudal septum and neck; in *E. minuta*, ovaries are short (Silas and Srinivasan, 1969) and straight. Pieces of brood sacs were observed hanging from oviducts of most species in the genus *Eukrohnia* (Alvariño, 1967, 1968). In *Krohnitta mutabbii* and *K. pacifica*, ovaries extend to a level close to the region of the ventral ganglion, and in some cases, might extend up to near the neck region, while in *K. subtilis*, ovaries are short, reaching only the anterior end of the paired fins. The ovaries of *Pterosagitta draco* are long, wide tubes which extend up to the anterior septum in the neck, completely filling the trunk cavity in fully mature specimens.

In species of the *Sagitta* group 'maxima' (*S. gazellae*, *S. lyra*, *S. maxima*, *S. scrippsae*), and in *S. hexaptera*, the ovaries reach up to the region of the

Table 1
Chaetognatha: length of ovaries and arrangement and size of ova

Species	Length of ovary	% of total length	Arrangement of ova	Size of ova (mm)	Average no. of ova per ovary
Eukrohnia bathyantarctica	2.7	8.9	2 lines	0.2	20
Eukrohnia bathypelagica	8.5	35	2 lines, occasionally 3	0.33	~42
Eukrohnia fowleri	4.8	12	2 lines	1.5	6–8
Eukrohnia hamata	7.7	18	4 lines, ending at top in 1 ovum	0.08	130
Eukrohnia minuta	1	< 10	1 line	0.11	11
Krohnitta mutabbii	2–2.6	35	1 line	0.15	~20
Krohnitta pacifica	3.5	56	1 line	0.1	18–20
Krohnitta subtilis	1.4–1.9	12	2 lines	0.2	12
Pterosagitta draco	3.6	50	2 lines	0.2	45
Sagitta gazellae	52	63	8 lines	0.6	800
Sagitta lyra	17	46	4 lines	0.2	> 200
Sagitta scrippsae	40	67	4 lines	0.5	> 300
Sagitta maxima	53	59	5 lines, ending in 1 at the top	0.3	> 400
Sagitta hexaptera	27	54	3 lines	0.5	~ 250
Sagitta enflata	First cycle 0.6	11	3 lines	0.16	12
	Last cycle 6	24	3 lines	0.2	> 100
Sagitta pulchra	13	57	2 lines, occasionally 3	0.1	~ 200
Sagitta bierii	4.6–5.6	33	2 lines	0.13	50
Sagitta pacifica	6–7	53	1 line	0.08	~ 50
Sagitta pseudoserratodentata	3–4	43	1 line	0.1	20
Sagitta serratodentata	5	48	1 line, occas. extra line	0.09	~ 40
Sagitta tasmanica	9–11	59	2 lines	1.4	~160
Sagitta bombayensis	4–5	30	1 line	0.1	30
Sagitta bruuni	6	44	2 lines	0.12	60
Sagitta crassa	2.6–2.8	19	1 line	0.13	18
Sagitta euneritica	3.9–5.8	39	3 lines	0.1	~120
Sagitta euxina	6	27	2–3 lines	0.2	70–80
Sagitta friderici	2	15	2 lines	1.3	50
Sagitta peruviana	7	59	2 lines	0.1	130
Sagitta popovicii	1.7	30	1 line	1.6	9–10
Sagitta setosa	1.5	10.8	2 lines	0.25	36
Satitta tenuis	1.8	23	2 lines	0.05	80
Sagitta bipunctata	5–6	36	2 irregular lines	0.1	70
Sagitta macrocephala	7–8	37	4 lines, ending in 1 at the top	0.17	150
Sagitta helenae	6.5–7	50	2 lines	0.1	120
Sagitta marri	14	52	2 lines	0.2	70
Sagitta planctonis	18	51	4–6 lines	0.2	> 400
Sagitta zetesios	25	60	3 lines	0.2	> 300
Sagitta bedoti	6.5	45	3 lines	0.8	150
Sagitta nagae	9–11	38	2 or 3 lines	0.16	150
Sagitta elegans	6.8–13.6	34	2 lines	0.30	90
Sagitta minima	1.1	11	1 line	0.2	~4
Sagitta decipiens	6	41	1 line	0.14	20
Sagitta ferox	10–12	67	3 lines	0.1	> 200

Table 2 (*cont.*)

Species	Length of ovary	% of total length	Arrangement of ova	Size of ova (mm)	Average no. of ova per ovary
Sagitta hispida	4–5	41	2 lines	0.1	80
Sagitta robusta	6–8	66	1 line	0.1	> 60
Sagitta tokiokai	10–14	67	4 lines	0.3	< 300
Sagitta neglecta	4	51	1 line	0.15	30
Sagitta regularis	2.4	41	1 line	0.2	12
Sagitta bedfordii	1–1.2	32	1 line	0.2	4–5
Sagitta johorensis	1.2	28	1 line	0.1	9–10
Sagitta oceania	3	47	1 line	0.2	10
Sagitta septata	3.5	59	1 line	0.1	30

ventral ganglion, except in S. *lyra*, in which they extend only three-quarters the length from the posterior septum to the ventral ganglion. In S. *enflata*, fully mature ovaries reach either two-thirds the extent of posterior fins on the trunk, or to the anterior end of posterior fins, or up to anterior fins, depending upon whether the specimens are in the first, second, or last maturity cycle. It was suggested, that this polymorphism could be genetically controlled. However, the presence of a few gigantic ova, and the fact that the conjunctive mesenteric cord attaching the ovaries to the body wall reached up to the level of the anterior fins (maximum extent of the ovary in the largest individuals) appear to indicate that these organisms undergo a continuous process of growth and ovarian maturation (Alvariño, 1963, 1967) at all locations inhabited by the species. In Fig. 2A, is shown an ovary with newly developing oocytes together with three abnormally large ova. The latter are probably remnants of the previous maturity cycle, which continued to receive a nutrient supply with the new ones. The S. *pulchra* ovaries reach, in fully mature individuals, the level of the ventral ganglion.

In species of the 'serratodentata' group (*S. bierii*, *S. pacifica*, *S. pseudoserratodentata*, *S. serratodentata*, and *S. tasmanica*), ovaries reach up to or about the level of midlength of anterior fins. In most neritic species (*S. bruuni*, *S. bombayensis*, *S. crassa*, *S. euneritica*, *S. euxina*, *S. friderici*, *S. peruviana*, *S. popovicii*, *S. setosa*, and *S. tenuis*), the ovaries reach various levels of the anterior fins; in *S. bruuni*, they extend up to the level of the anterior quarter of the anterior fins. The conjunctive mesenteric filament (clearly visible in this species) extends to the level of the anterior end of the ventral ganglion, which indicates the possibility that the ovaries may reach a level close to that region. In the 'bipunctata' group, *S. bipunctata* ovaries are long, reaching the anterior third of the anterior fins, and in *S. helenae* and *S. macrocephala*, ovaries reach the level of the ventral ganglion. In the group 'planctonis', the *S. marri* ovaries extend to a region close to the ventral ganglion, while those of *S. planctonis* and *S. zetesios* extend to the neighbourhood of the neck.

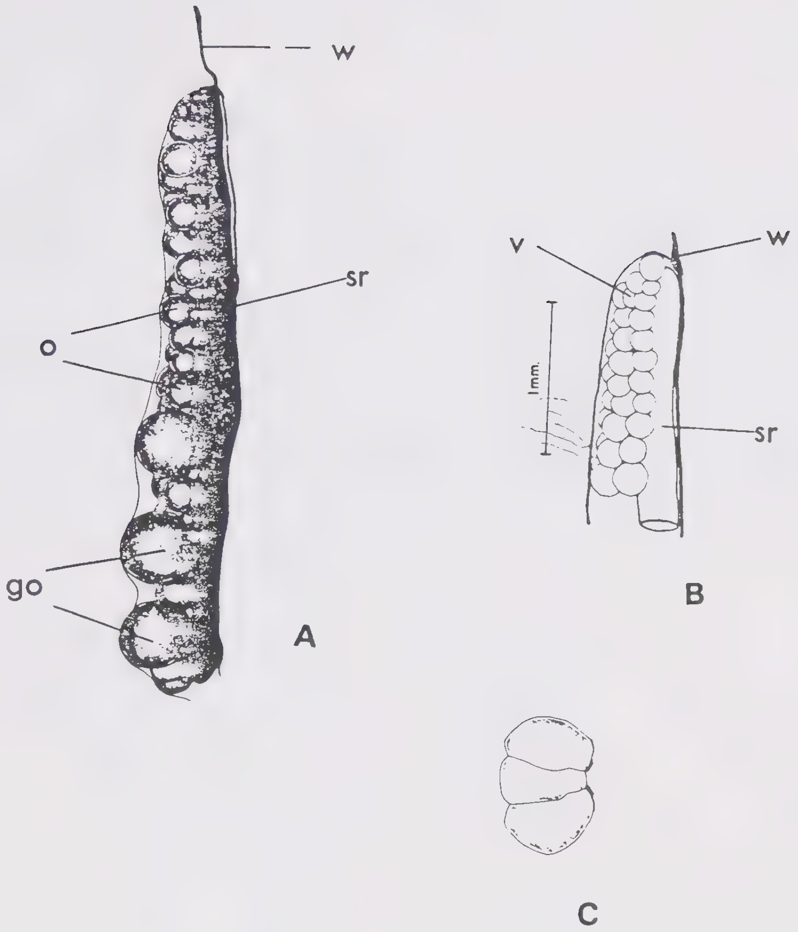

Fig. 2. (A) Dorsoventral view of ovary and ova of *S. enflata*, in second cycle of maturity. Giant ova remain from previous maturity cycle. (B) Dorsoventral view of ovary and ova of *S. macrocephala*; (C) upper view of disposition of ova in ovary of *S. tokiokai*. go, Giant ova; o, developing ova; sr, seminal receptacle filled with sperm in (A), empty in (B); v, ova; w, conjunctive or mesenteric cord attaching ovary to the body wall

In the 'bedoti' group, the ovaries of *S. bedoti* reach the region of the ventral ganglion, and in *S. nagae* to the anterior end of the anterior fins. In the group 'elegans', they extend to the anterior half of the anterior fins (*S. decipiens* and *S. elegans*); in *S. minima*, they are short, reaching the anterior middle part of the posterior fins. In species of the group 'hispida', the ovaries of *S. ferox*, *S. robusta*, and *S. tokiokai* extend to the neck region, and those of *S. hispida* to the region of the ventral ganglion. In the 'neglecta' group (*S. neglecta* and *S. regularis*), the ovaries extend to the region of the ventral ganglion. Finally, in the group 'oceania', the ovaries reach the level of the ventral ganglion in

S. bedfordii, *S. johorensis*, and *S. oceania*, but in *S. septata*, they extend to the neck.

III. ORIGIN OF FEMALE GERM CELLS

The germ cells of chaetognaths, discovered by Butschli (1873), can be distinguished early in development. He described in the gastrula of *Sagitta*, pluricellular formation at the bottom of the archenteron and identified it as the primordium of the germinal line. Hertwig (1880), however, stated that this 'anlage' was formed at first by two cells. Apparently, segregation of the germinal line is still more precocious, being present in unsegmented newly laid eggs. The discrepancy found by various authors is probably due to differences in fixation and the time at which the germ cell determinant has been observed.

In chaetognaths, Elpatiewsky (1913) was the first to describe the structure of the germ cell determinant; Buchner (1910), Ghirardelli (1953a,b), Stevens

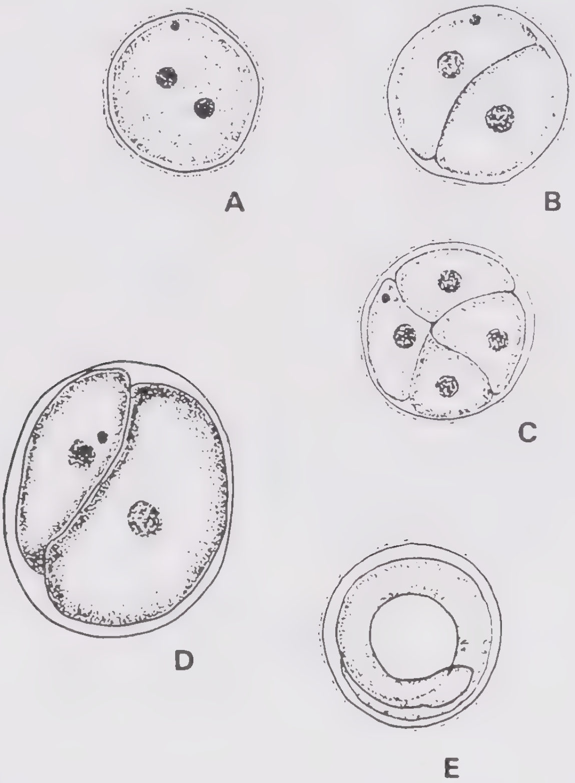

Fig. 3. Development of the egg. (A, B) The germinal cell can be observed as a dot at the top; in (C) it is at the top left; (D) indicates the two blastomeres and the identification of the germinal blastomere; (E) doubly coiled embryo in the egg of a chaetognath

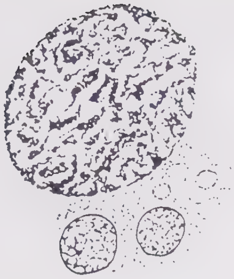

Fig. 4. Representation of micrograph of germ cell determinant of *Spadella cephaloptera*

(1910), and Vasiljev (1924) also studied this formation. The germ cell determinant can be usually seen near the periphery of the egg, often surrounded by large yolk globules, in a well-defined boundary, although no membrane is present to isolate it from the cytoplasm. The germ cell determinant appears as an irregularly shaped, more or less branched filamentar mass, with large grains and plaques all tangled together. The constituents do not seem to be homogeneous, but form loops of various forms and variable opacity, due to the different nature of the formations. Grains and small plaques tend to settle around the nucleus of the germ cell.

The germ cell divides into two unequal portions (Stevens, 1910; Elpatiewsky, 1913) which divide further during or after gastrulation, forming four cells. The spermatogonia are derived from the cell receiving less quantity of the determinant, while oogonia originate from the largest cell. On hatching, two primitive cells situated in front of the caudal septum give rise to the female line (ovary, ova, and receptaculum seminis), and the other two situated behind the septum give rise to the male germ line (testis, sperm, and seminal vesicles). The primitive germ cell in the gastrula and larva of *Sagitta* is easily recognizable *in vivo* by its large size and typical voluminous nucleus. In *Spadella cephaloptera*, by destroying the blastomere containing the germ cell determinant with a fine needle, it was possible to demonstrate that the other blastomere may provide a gastrula devoid of germ cells (Ghirardelli, 1954) (see Figs. 3 and 4).

IV. ARRANGEMENT OF OVA IN THE OVARY

The ova are arranged in the ovaries in linear rows. The number of rows of ova per ovary is a specific characteristic and ranges from 1 to 8 per ovary (Figs. 5–18). In species of *Spadella*, benthic in habits, ova are few, but large and arranged in one row along the ovary. The number of ova per ovary ranges from 3 or 4 in small tropical species and in *Spadella*, to more than 800 in *S. gazellae*, an Antarctic species. In tropical species with short life span and a continuous reproductive cycle, and in species which protect the eggs by laying them in pouches (*Eukrohnia*), or in clutches in sheltered locations (*Spadella*), the ova are fewer and larger than in species of cold and temperate waters

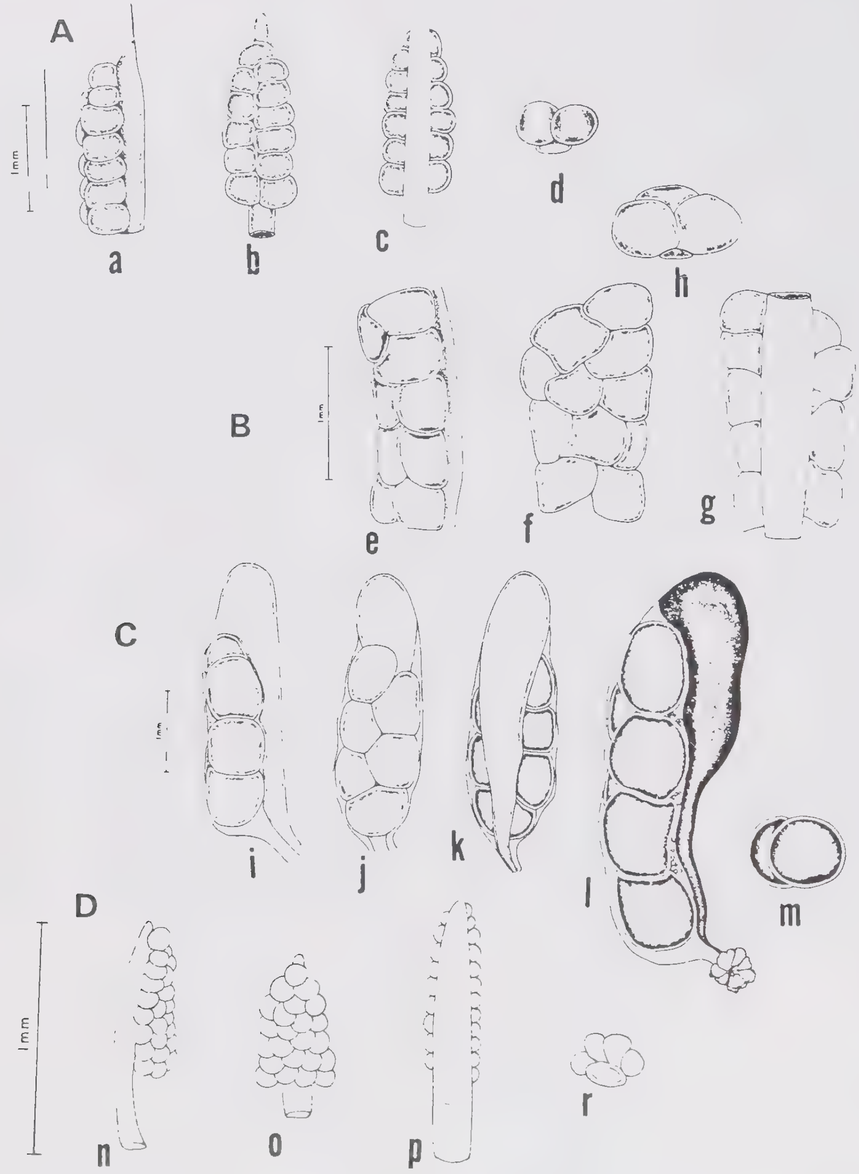

Fig. 5. Disposition of the ova in the ovary of (A) *Eukrohnia bathyantarctica*, and (B) *E. bathypelagica;* (C) *E. fowleri;* (D) *E. hamata*. a, e, i (stage 3), and n, dorsoventral view; b, f, j, and o, latero-internal view; c, g, k, and p, latero-external view; d, h, m, and r, upper view; l, dorso-ventral view of stage 4. Note the well-developed seminal receptacle in all the four species. (From Alvariño, 1967, 1969.)

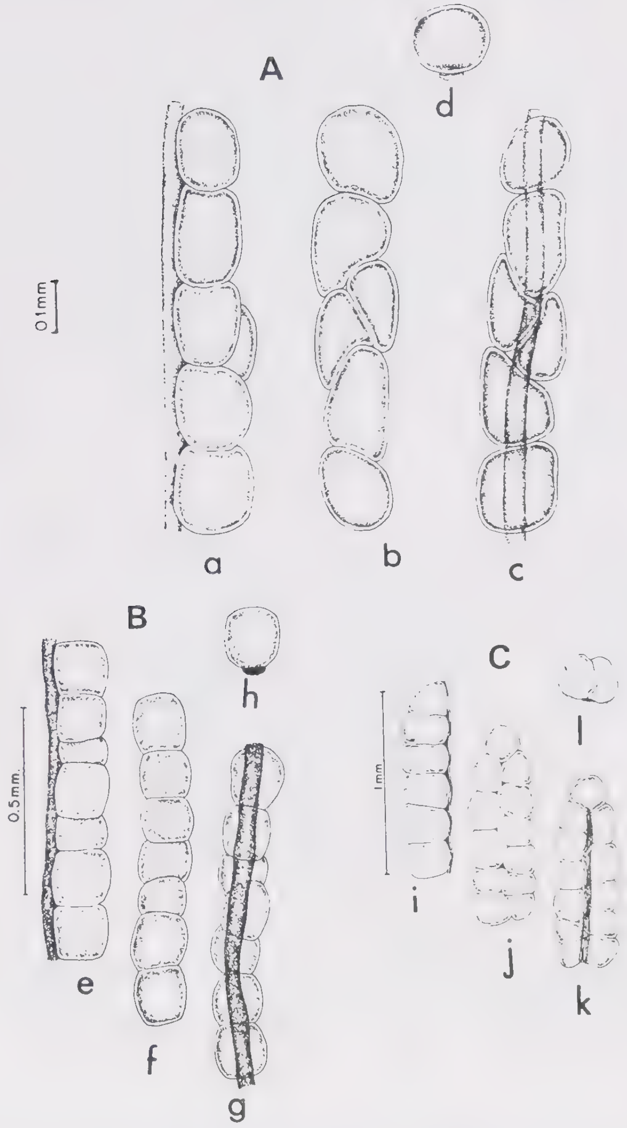

Fig. 6. Disposition of the ova in the ovaries of (A) *Krohnitta mutabbii*, (B) *K. pacifica*, and (C) *K. subtilis*. a, e, and i, Dorsoventral view; b, f, and j, latero-internal view; c, g, and k, latero-external view; d, h and l, upper view. (From Alvariño, 1963, 1967, 1969.)

laying the eggs freely in the sea. The size of the ova is reflected on the size of the embryo and the larva; larger larvae are stronger than small-sized ones, but in warm waters, development of small larvae is fast, due to increase in metabolic rate.

In Table 1 are included most of the pelagic species of chaetognaths, and

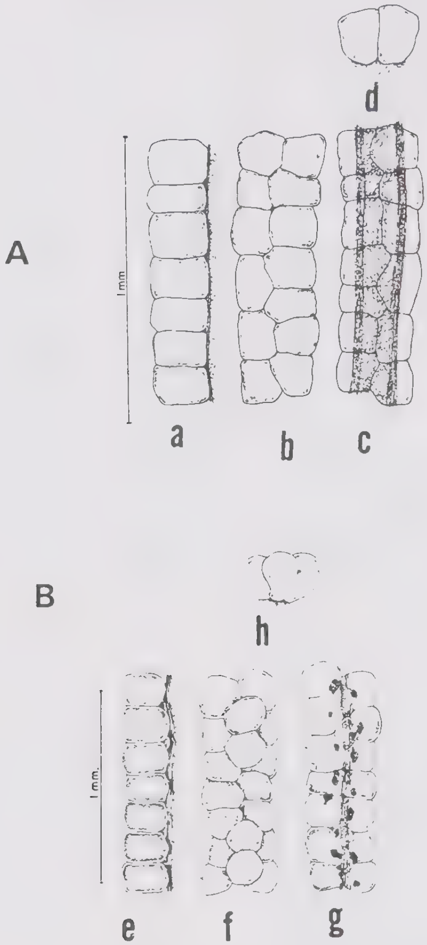

Fig. 7. Disposition of the ova in the ovaries of (A) *Pterosagitta draco*, and (B) *Sagitta pulchra*. a, e, Dorsoventral view; b, f, latero-internal view; c, g, latero-external view; d, h, upper view. (From Alvariño, 1967, 1969.)

information on the length of the ovaries, the percentual length the ovaries occupy in terms of the total length of the animal, arrangement of ova in the ovaries, size of the ova, and average number of ova per ovary. The strategic role of ova and ovaries in the ecology of the species and in the abundance of chaetognath populations is discussed elsewhere (Alvariño, Volume VI).

The relationship between ovary length and size of the ova (see Table 1) indicates the number of gametes which will be potentially transformed into eggs and produce a new generation. The average length of ripe ovaries (Russell, 1932) of adult *S. elegans* of different sizes and the ratio of their ovary length to total body length show that in small adults the length of the ovary is less in

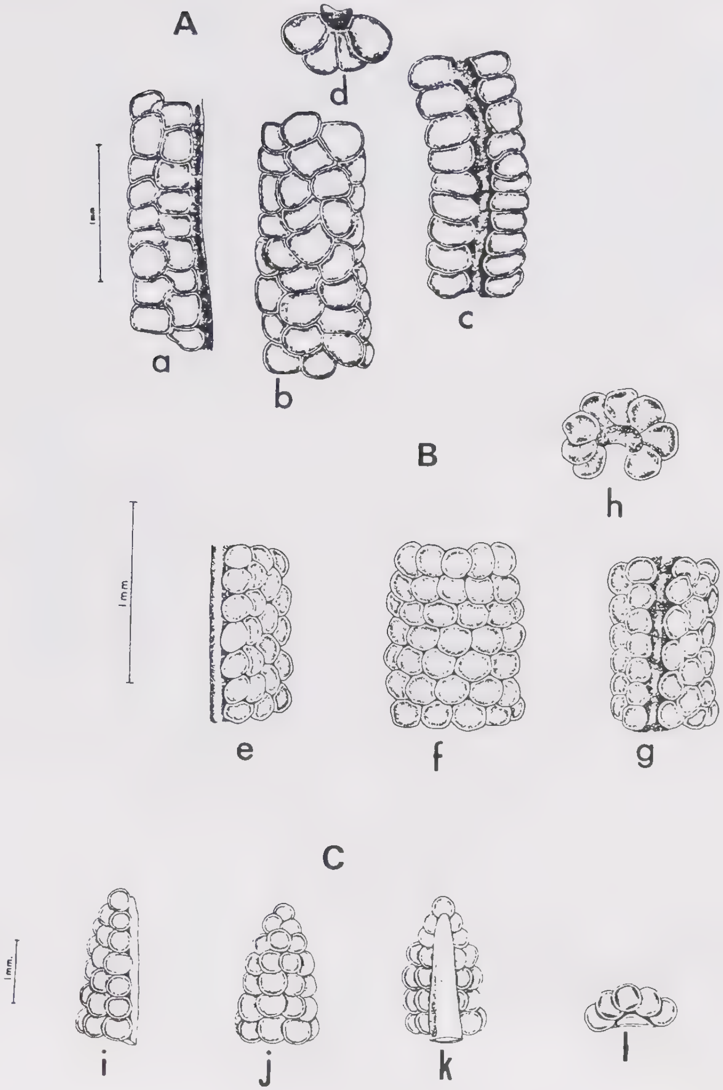

Fig. 8. Disposition of the ova in the ovaries of (A) *Sagitta lyra*, (B) *S. gazellae* and (C) *S. maxima*. a, e, and i, Dorsoventral view; b, f, and j, latero-internal view; c, g, and k, latero-external view; d, h, and l, upper view. (From Alvariño, 1967, 1969.)

proportion to the total length of the body than in large adults. There is no evidence of any marked decrease in diameter of ripe ova at different times of the year. Therefore, the number of eggs produced per individual must be greatest during the early months of the year, when the adults reach their largest size; in later summer, eggs are few due to the small size of the breeding individuals.

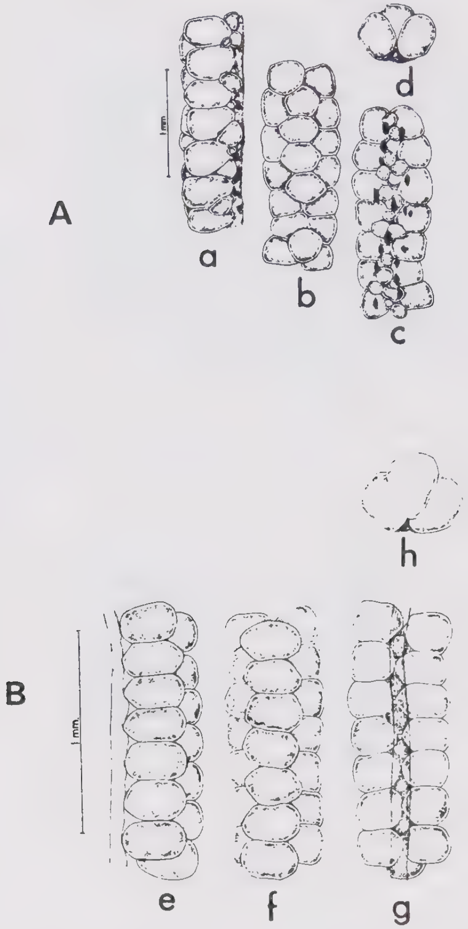

Fig. 9. Disposition of the ova in the ovaries of (A) *Sagitta hexaptera* and (B) *S. enflata*. a, e. Dorsoventral view; b, f. latero-internal view; c, g, latero-external view; d, h, upper view. (From Alvariño, 1963, 1967, 1969.)

V. OOGENESIS

The oogonium gives rise to a primary oocyte which has a diploid chromosome number. After a period of growth, when the primary oocyte has reached about the size of the mature ovum, meiotic division or first maturation division takes place, resulting in a large daughter cell and a small abortive first polar body. The secondary oocyte divides again, forming the ovum and a secondary daughter cell or second polar body which degenerates. In this way, the chromosome number is reduced to haploid.

Oogenesis has been described for *S. elegans* (Stevens, 1910), *S. bipunctata* (probably *S. friderici* or *S. elegans*) (Stevens, 1905, 1910; Bordas, 1920, see

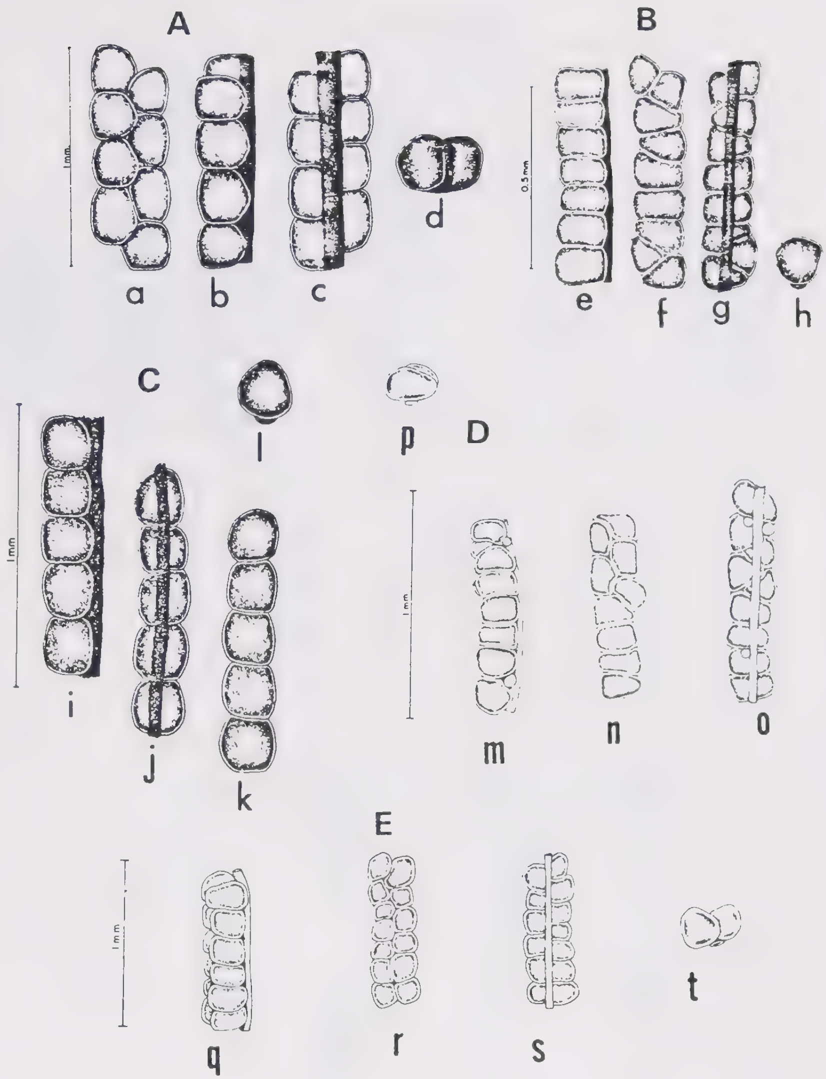

Fig. 10. Disposition of the ova in the ovaries of (A) *Sagitta bierii*, (B) *S. pacifica*, (C) *S. pseudoserratodentata*, (D) *S. serratodentata*, and (E) *S. tasmanica*. a, e, i, m and q, Dorsoventral view; b, f, j, n and r, latero-internal view; c, g, k, o and s, latero-external view; d, h, l, p and t, upper view. (From Alvariño, 1963, 1967, 1969.)

also 1912), *S. bipunctata* (Burfield, 1927), *Spadella cephaloptera* (Vasiljev, 1924; John, 1933) and *Pterosagitta draco* (Ghirardelli, 1968). Oocytes of all size classes may be connected to suspension cells, which serve to absorb substances from the mucoid syncytium, a thin layer with mucoid structure and serving as feeding substance for developing oocytes. Maturation and growth of

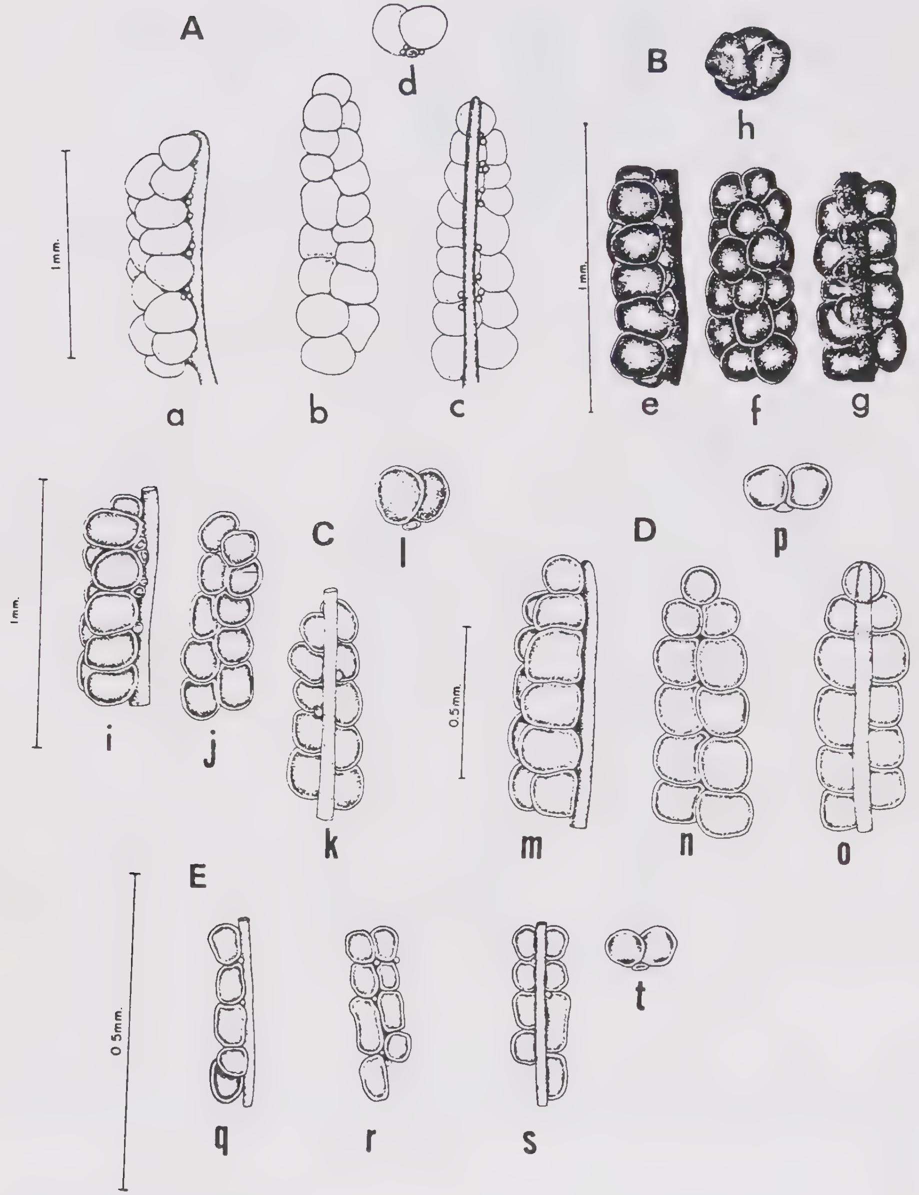

Fig. 11. Disposition of the ova in the ovaries of (A) *Sagitta bruuni*, (B) *S. euneritica*, (C) *S. friderici*, (D) *S. setosa*, and (E) *S. tenuis*. a, e, i, m, and q, Dorsoventral view; b, f, j, n, and r, latero-internal view; c, g, k, o, and s, latero-external view; d, h, l, p, and t, upper view. (From Alvariño, 1963, 1967, 1969.)

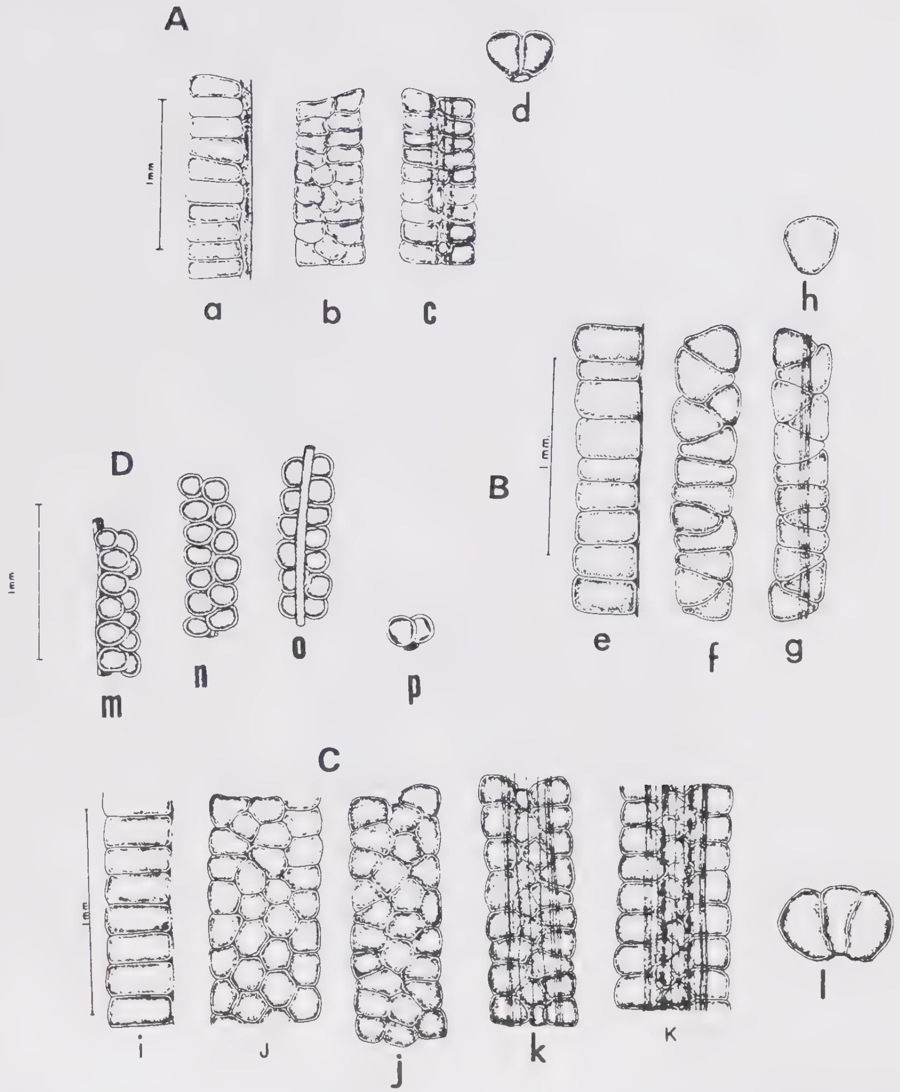

Fig. 12. Disposition of the ova in the ovaries of (A) *Sagitta ferox*, (B) *S. robusta*, (C) *S. tokiokai*, and (D) *S. hispida*. a, e, i, and m, Dorsoventral view; b, f, j, and n, latero-internal view; c, g, k, and o, latero-external view; d, h, l, and p, upper view. (From Alvariño, 1967, 1969.)

oocytes have been described by Stevens (1905) and Bordas (1920) who indicated that the ovaries might include oocytes of various sizes. These authors studied the so-called nuclear net, a series of grains and small plaques appearing in the oocytes during their first period of growth (about 10–15 μm in diameter), with nucleus at a late pachytene stage. These structures appear to be, according

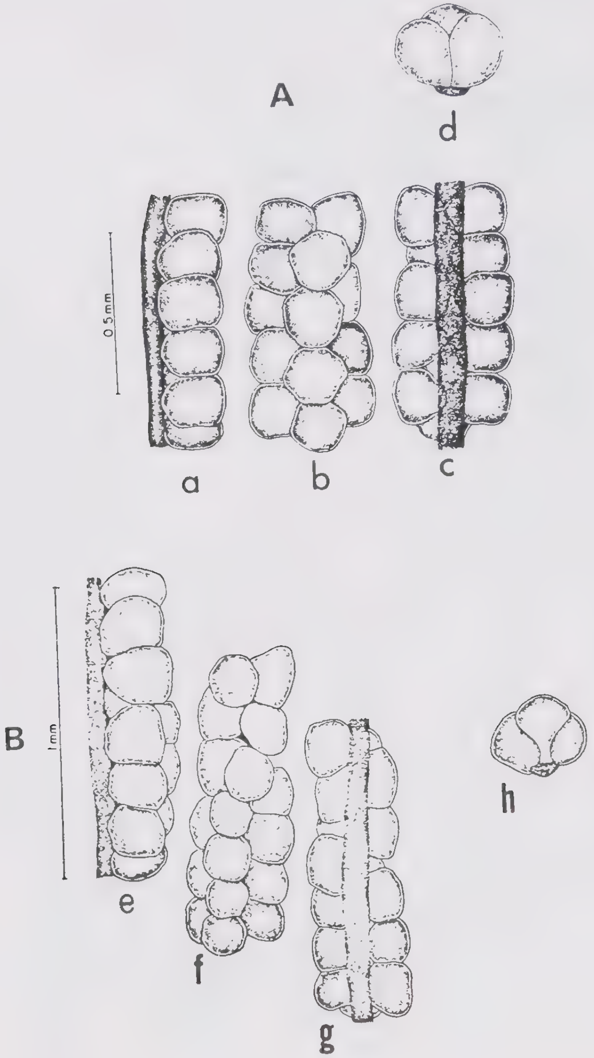

Fig. 13. Disposition of the ova in the ovaries of (A) *Sagitta bedoti* and (B) *S. nagae*. a, e, Dorsoventral view; b, f, latero-internal view; c, g, latero-external view; d, h, upper view. (From Alvariño, 1967.)

to Ghirardelli (1968), abundantly supplied with RNA, some polysaccharides, and proteins. No nucleolus was observed in the ova of *S. cephaloptera* (Ghirardelli, 1961; Ghirardelli and Brandi, 1961), which indicates that the functions of the nucleolus are probably assumed by the small plaques of the so-called nuclear net. Granulation begins to appear inside the nuclear membrane, giving at times the impression of these formations entering into direct contact with the cytoplasm. Their number increases during the second

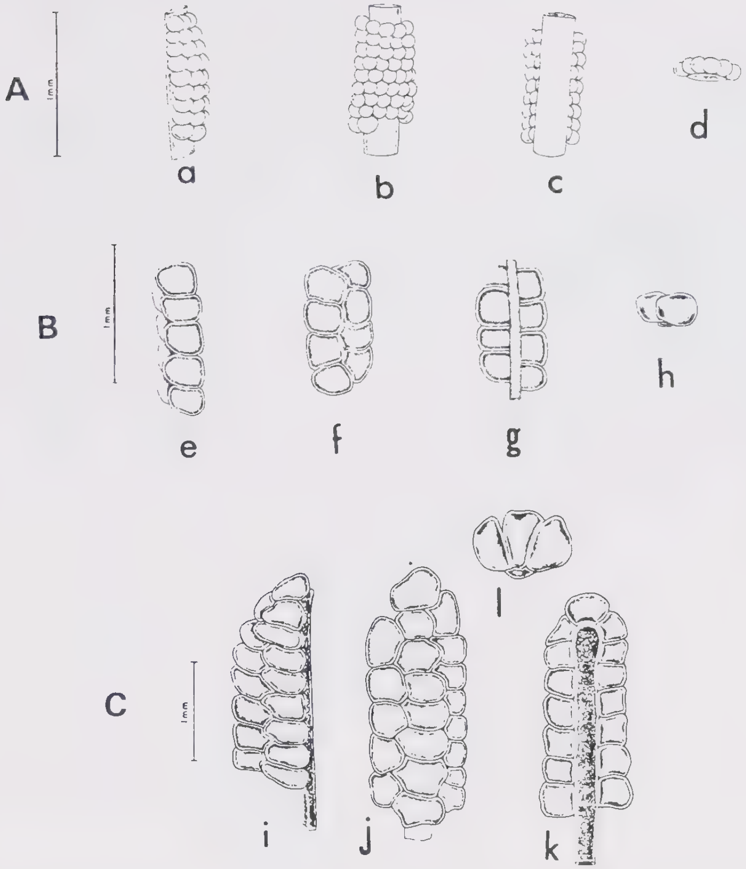

Fig. 14. Disposition of the ova in the ovaries of (A) *Sagitta planctonis*, (B) *S. marri*, and (C) *S. zetesios*. a, e and i, Dorsoventral view; b, f and j, latero-internal view; c, g and k, latero-external view; d, h, and l, upper view

period of growth (oocytes > 30 μm in diameter) when synthesis of the specific yolk protein is most active.

A relation has been observed (Ghirardelli, 1961) between the quantity of RNA present in plaques of the nuclear net and in the cytoplasm. During the first period of growth, i.e. when the nucleus is in the synaptic stage, there is an increase in RNA content of the cytoplasm; RNA is often distributed in concentric rings around the nucleus. During vitellogenesis, both cytoplasm and small plaques of nuclear net have less RNA. The greatest concentration of RNA generally occurs in small oocytes located near the seminal receptacle. This may support the hypothesis of Bordas (1920) that the seminal receptacle may have trophic functions, producing substances which may affect the development of oocytes.

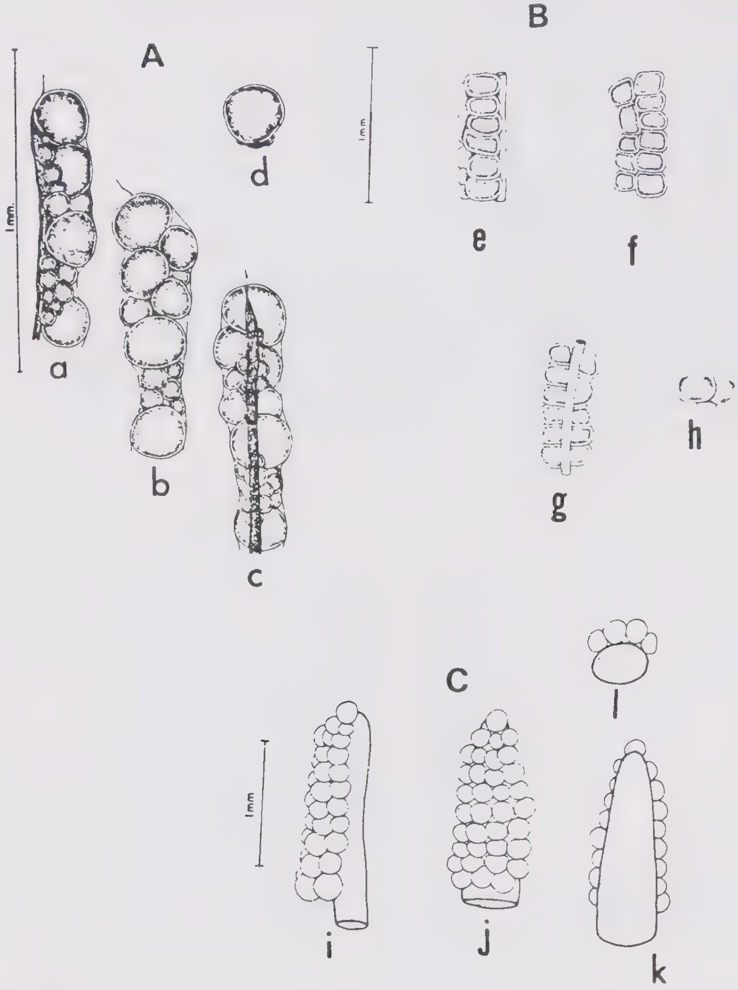

Fig. 15. Disposition of the ova in the ovaries of (A) *Sagitta bipunctata*, (B) *S. helenae*, and (C) *S. macrocephala*. a, e, and i, Dorsoventral view; b, f, and j, latero-internal view; c, g, and k, latero-external view; d, h, and l, upper view

VI. GONAD INDEX

The most widely used and simple quantitative method for estimating reproductive activity is the gonad index, which is basic in handling large numbers of individuals (Giese and Pearse, 1974). It is calculated in various ways, but is usually the ratio of the gonad wet weight or volume to wet weight or volume respectively of the whole animal. This method may be adequate for some animals, but cannot be used for chaetognaths.

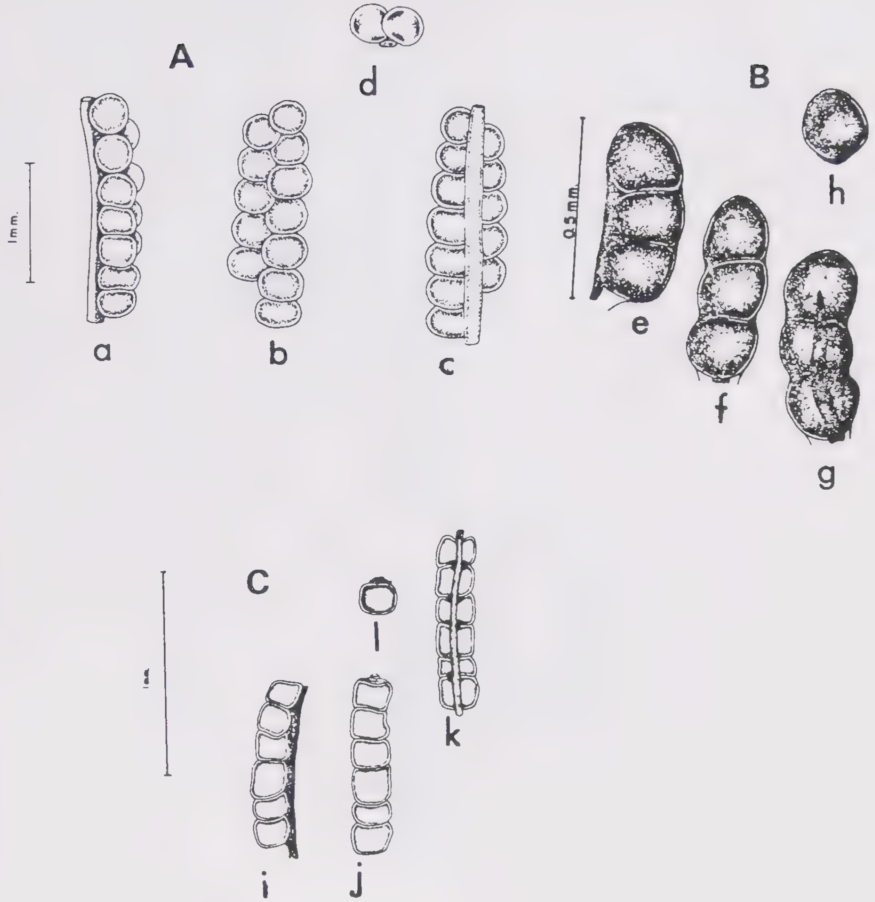

Fig. 16. Disposition of the ova in the ovaries of (A) *Sagitta elegans*, (B) *S. minima*, and (C) *S. decipiens*. a, e, and i, Dorsoventral view; b, f, and j, latero-internal view; c, g, and k, latero-external view; d, h, and l, upper view. (From Alvariño, 1963, 1967, 1969.)

Chaetognaths are transparent to translucent animals, and the gonad index can be estimated by measuring the length of the ovaries in relation to the length of the animal and the size and number of ova per animal. The male gonad index is easily measured by the development of the seminal vesicles, but this does not seem to have a definitive correlation to reproduction. On the other hand, the female gonad index has a direct significance in the population, inasmuch as the relative reproductive condition of animals of variable size can be measured and changes in gonads at different times detected. Combined with histology, the gonad index is valuable in assessing reproductive changes in chaetognath populations.

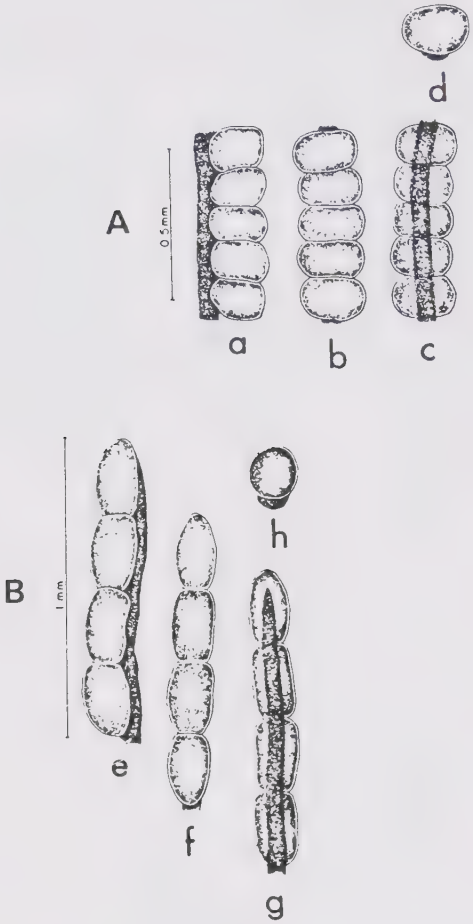

Fig. 17. Disposition of the ova in the ovaries of (A) *Sagitta neglecta* and (B) *S. regularis*. a, e, Dorsoventral view; b, f, latero-internal view; c, g, latero-external view; d, h, upper view. (From Alvariño, 1963, 1967, 1969.)

VII. THE EGG

Chaetognath eggs are transparent and contain abundant yolk, the most transparent being those of *Sagitta enflata*. The eggs of *Spadella* have an elastic shell that can be removed, but the vitelline membrane is delicate. Electron microscope studies by Ghirardelli (1968) show that the eggshell is comprised of two well-defined layers, an external fibrillar layer 0.1 μm across, and an internal granular layer which is thicker. The vitelline membrane which is elastic has three layers closely connected with the cytoplasm (Ghirardelli, 1963). The structure of the membrane may perhaps explain the difficulty in separating the two blastomeres experimentally.

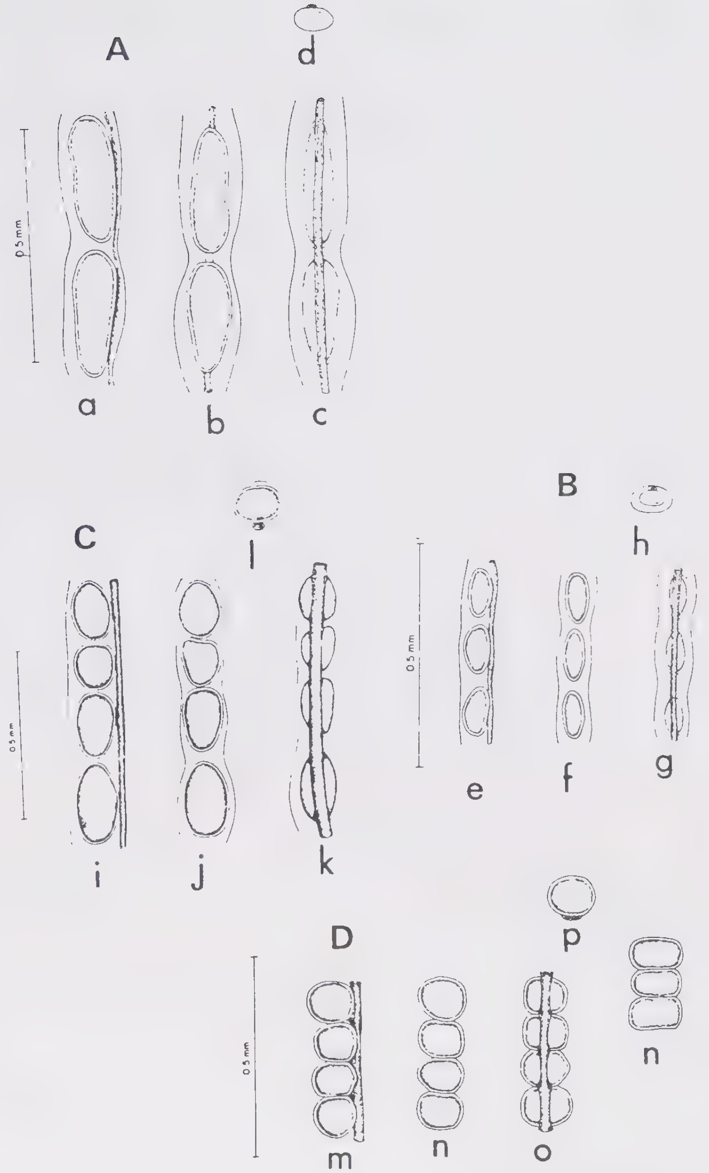

Fig. 18. Disposition of the ova and part of ovary of (A) *Sagitta bedfordii*, (B) *S. johorensis*, (C) *S. oceania*, and (D) *S. septata*. a, e, i, and m, Dorsoventral view; b, f, j, and n, latero-internal view; c, g, k, and o, latero-external view; d, h, l, and p, upper view. (From Alvariño, 1967.)

The eggs of *Sagitta crassa* and *S. bipunctata* are enclosed by a firm transparent shell and have a large vitelline space. The eggs of *S. enflata*, *S. elegans*, *S. ferox*, *S. hispida*, and *S. minima* are likewise surrounded by a firm membrane, but a perivitelline space is absent.

Egg size is in part phenotypically determined, and is in part under genetic control. Large eggs generally produce large larvae. Planktonic organisms from cold waters produce large larvae and juveniles, which are best adapted to search for food (Barnes and Barnes, 1968). The fertilized ova of *S. nagae* measure 0.16–0.20 mm at deposition, and 0.18–0.28 mm in diameter when fixed more than 10 hours later (Nagasawa and Marumo, 1978). The eggs of *P. draco* measured 0.36–0.40 mm (Sanzo, 1937), and those of *S. elegans* from the Gulf of Maine (Sherman and Schaner, 1968), Bay of Fundy and Gulf of St. Lawrence (Huntsman and Reid, 1921), 0.33 mm and from Bedford Basin 0.31 to 0.34 mm (Zo, 1973). The *S. setosa* eggs from the Black Sea ranged from 0.333 to 0.379 mm, and those of *S. euxina* were 0.30 mm in diameter (Elian, 1960). The *S. bipunctata* eggs are 0.20 mm, and those of *S. crassa* 0.35 mm (Murakami, 1959). Studies by Alvariño (1968) show that eggs of species belonging to the more advanced genus are probably the best equipped for survival.

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27. CHAETOGNATHA

ANGELES ALVARIÑO
7535 Cabrillo Avenue, La Jolla, California 92037, U.S.A.

I. INTRODUCTION

The Chaetognatha, generally called arrow-worms, are hermaphrodites; the testes are in the tail, totally independent of the ovaries. The male reproductive system—which comprises the testes, vasa deferentia, and seminal vesicles—occupies completely the coelom of the caudal segment, except in *Sagitta enflata*. In this species, the testes occupy the posterior half of the tail segment. The tail segment is divided into a right and a left chamber by the dorsoventral mesentery. At the centre of each chamber is a median longitudinal wall (secondary mesentery) extending along each half of the tail segment, and held ventrally and dorsally. This secondary mesentery does not divide completely the right or the left chamber; and the material contained in each left and right part of the tail segment can circulate freely and independently. The right and left chambers do not communicate with each other; each chamber is occupied by one testis.

II. TESTIS

The testis (Fig. 1) is covered by a thin layer of endothelium continuous with the body wall along the line of attachment. In young animals approaching sexual maturity, testes are full of sperm-mother cells which grow and develop floating in the fluid filling the tail cavity. Testes in adult animals are filled with masses of spermatozoa at various stages of development. Groups of spermatogonia develop from the germinal layer in testes, and give rise to spermatocytes, spermatids, and finally spermatozoa which gradually fill the testes in the tail cavity.

In the testes are masses of sexual elements, all at the same or nearly the same stage of development (Bordas, 1914; Ghirardelli and Arnaud, 1966). However, different stages of spermatogenesis can also coexist in the testes. The masses of sperm formations are continuously on the move in the testes. The speed of movement varies with species and with the degree of fullness of the testes, and is enhanced by temperature. In *Spadella*, circulation is slower than in *Sagitta bipunctata* and related species (Ghirardelli; 1968).

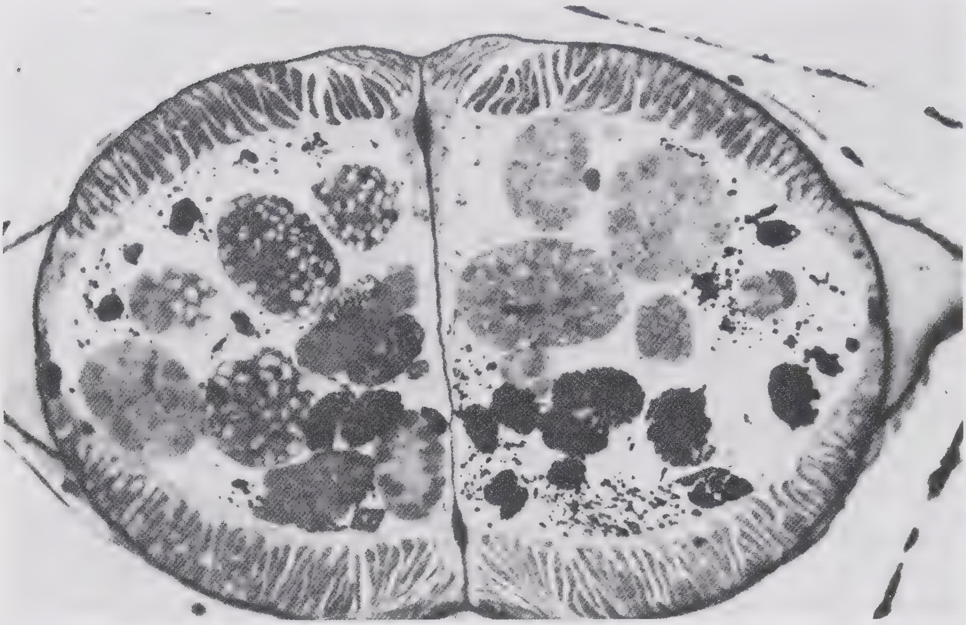

Fig. 1. Cross-section through the testes of *Sagitta euneritica*. (Courtesy: Dr. Bernhard E. F. Reimann). (×410)

As can be seen from Fig. 2, in each chamber of the tail cavity, spermatogonial masses and spermatozoa move forward along the outer side, pass around the anterior end of the secondary mesentery, and then move towards the tip of the tail alongside the median longitudinal mesentery of the tail. Interestingly, small isolated masses of spermatocytes move very rapidly when close to the median longitudinal mesentery, which indicates this mesentery might be ciliated. Spermatogonia and developing spermatozoa seem to be kept in continuous movement in the testis cavity by ciliated cells of the lateral line and median mesentery. Spermatocytes, arranged in groups ('polyplasts' of Bordas, 1912, 1914), are separated from each other by the trabeculae in testicular space. The movement is circulatory and can be easily observed; it is not straight, as schematically illustrated in Fig. 2, but tortuous, following the irregularities of the paths interlocked among the trabeculae of spongy mesh structure. Burfield (1927) indicates that the movement of 'polyplasts' is due to the activity of the ciliated cells covering the median mesentery, whereas Bordas (1912, 1914) considers it is due to the tail action of mature spermatozoa. Interestingly, spermatocytes circulate even when the spermatozoa are absent. It is suggested that circulation could be also helped by ciliation at the opening of the vas deferens. With approaching maturity this meshwork, with its numerous groups of spermatocytes, fills up the whole space of the tail cavities.

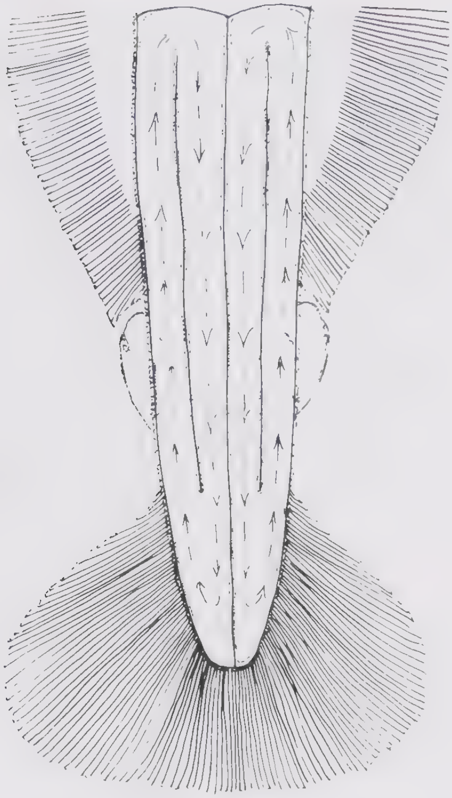

Fig. 2. General circulation of spermatozoa in testes of chaetognaths

The progressive development of the spermatocytes is almost synchronous; they all divide together into spermatids and these differentiate into spermatozoa. As the testis matures, groups of spermatozoa are distinctly visible among the spermatocytes. The formation of spermatozoa (Alvariño, 1965) starts at the anterior part of the testis, but a number of ripe spermatozoa may be found in the posterior part of the testis even while groups of spermatocytes are present anteriorly. Kramp (1917) considered an animal to be ripe, 'when ripe polyplasts are found through the whole length of the testes'. Spermatozoa are orientated in the testis with their head towards the anterior part of the animal; that is, facing the transverse wall.

The vas deferens communicates each testis with the seminal vesicle (Section V) of that side. These ducts are relatively long and may be shorter, longer, or about the length of the seminal vesicle. The sperm duct is lined with a simple epithelium (Burfield, 1927) and opens anteriorly into the tail coelom by an oval opening with slightly thickened lips; it proceeds down partially embedded in the body wall of the lateral line and opens by a ciliated opening into the seminal vesicle.

III. SPERMATOGENESIS

Spermatogenesis in the Chaetognatha has been studied mainly by Hertwig (1880), Bolles-Lee (1888), Stevens (1903, 1910), Bordas (1912, 1914), Tuzet (1931), and Ghirardelli (1954). The species studied is *Sagitta friderici*, and not *Sagitta bipunctata* as stated by these authors. *Sagitta friderici* is abundant at locations sampled by them, while *Sagitta bipunctata* is an oceanic species of scanty populations, not found at locations where the samples were obtained.

Chromosomes are 3 μm long, but in secondary spermatocytes they are only slightly over 1 μm long. Eighteen chromosomes (diploid number), about 3 μm long, were observed in *Sagitta friderici* (Boveri, 1890), *Sagitta enflata* (Buchner, 1910; Ghirardelli, 1954), *Sagitta minima* (Ghirardelli, 1954), *Sagitta elegans* (Stevens, 1910), and *Spadella cephaloptera* (Ghirardelli, 1959). Some differences may appear in the karyogram of various species. For instance, during spermatogonial metaphase of *Sagitta enflata*, five pairs of metacentrical chromosomes were observed (Ghirardelli, 1954), while in *Sagitta setosa* there were only four pairs. The squash technique confirms that, apart from small differences in detail, meiosis in *Sagitta setosa* follows the classic scheme (Ghirardelli and Arnaud, 1966). The X pair of chromosomes (Stevens, 1910) are named m chromosomes by Ghirardelli and Arnaud (1966) to avoid any confusion with the sex chromosomes. At the first metaphase, a pair of chromosomes moves more precociously than the others towards the opposite extremities of the thread spindle much like the sex chromosomes. Although these chromosomes cannot be considered strictly as sex chromosomes, the animal being hermaphroditic, this phenomenon was observed only during spermatogenesis and not in oogenesis.

Spermatogonia have a clear reniform nucleus (Tuzet, 1931) with one or two nucleoli. Chromatin appears in small roundish packs. The young spermatids have horseshoe-shaped dictyosomes and one or many small, granular chondriokonts, two of which are sometimes attached to form a large ball (mitochondrial balls).

During the so-called 'resting stage', in the nucleus of spermatids, the chromatin is irregularly netted, but suddenly a crown of condensed chromatin is formed along the periphery of the nucleus, until the whole nucleus is a sphere of chromatin of pycnotic characteristics. The elongated nucleus reaches close to the proximal and distal centrioles, which are connected. The proximal centriole is associated with the acrosome; the distal one gives rise to the caudal flagellum.

IV. THE SPERMATOZOA

Spermatozoa of chaetognaths are elongated thin filaments (Tuzet, 1931; Jägersten, 1940) with a long and fine acrosome at the anterior end. The proximal centriole is at the base of the acrosome, followed by chromatin filament; next is the short middle piece; and the caudal flagellum is short and placed towards one side. The spermatozoa of *Spadella* (Fig. 3) and *Sagitta* (Figs. 4 and 5) share some peculiar characteristics (Ghirardelli, 1968). They are both elongated with a centriole at the base of the long and thick acrosome, and are provided with an external chromatin thread placed at the side of the head, connected to the proximal centriole. The middle piece and the caudal flagellum are short in relation to the size of the head. Retzius (1909) gave a different description of the spermatozoa, in which the anterior part was reported as posterior and *vice versa*, and this research has now only historical value. Jägersten (1940), who studied chaetognath spermatozoa, indicated that isolated spermatozoa in water are unable to move. This is not true: I have observed such movement of spermatozoa in living *Sagitta enflata* and *Sagitta euneritica* studied under the microscope; they moved rapidly in water propelled by undulation of their tails. In these experiments, the spermatozoa flowed out in a current from the bursting seminal vesicles and spread like the flow of water from a hose; no spermatophore was formed.

Van Deurs (1972) studied mature spermatozoa of *Spadella cephaloptera*, and indicated that they corresponded to the filiform type, common to cirripedes, ostracods (see Pochon-Masson, this volume), insects, and other arthropods and also to gastropods (see Maxwell, this volume). However, the fine structure of the spermatozoa of the Chaetognatha (Fig. 5) does not agree with the ultrastructure described for any other filiform spermatozoon.

Most of the spermatozoa in the seminal vesicles of *Spadella cephaloptera* and also *Sagitta euneritica* are orientated in a direction parallel to the longitudinal axis of the seminal vesicle and the whole animal. Mature spermatozoon is approximately 290 μm long and 0.7 μm wide. Usually, the spermatozoon is orientated for definition laying ventrally; the median plane is vertical to the axoneme. At the anterior end of the spermatozoon are the membrane cap, acrosomal structure, and beaded vesicles; at the top is the centriole-like structure from which extends the axoneme running along the spermatozoon (Fig. 3). A few microns behind the centriolar region begins the long mitochondrion (about 250 μm) which extends along the spermatozoon till almost the end of the nucleus. Next to the beaded structure are the longitudinal sacs, at the central half of the spermatozoon between the mitochondrion and axoneme and continuing with the nuclear region and extending farther back than the mitochondrion. At the other end of the spermatozoon is a free flagellum, about 20 μm long.

The membrane cap is a complicated structure, 60 μm long at the anterior end of the sperm. It may be divided into four regions: (1) terminal region (1–2 μm), (2) centriolar region, (3) the axoneme, (4) axoneme and mitochondrion. The membrane cap is formed of two membranes in a double ring. The beaded structure, which extends for 50 μm, starting 8 μm off the top front, appears associated with the cap. The terminal region is in front of the centriolar region,

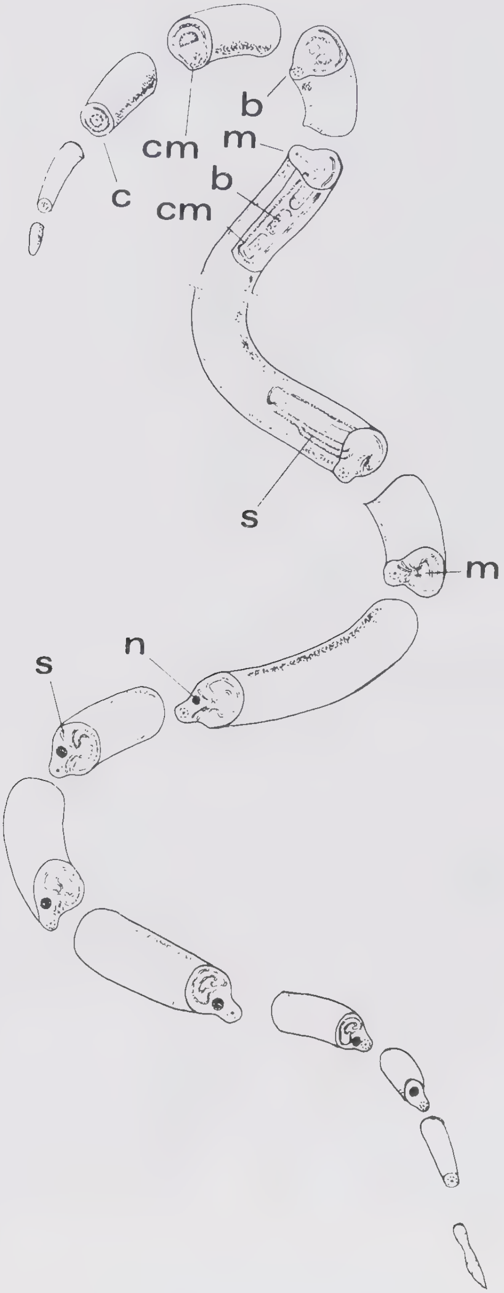

Fig. 3. Structure of mature spermatozoon of *Spadella* (after van Deurs, 1972). b, Beaded structure; c, centriolar structure; cm, membrane cap; m, mitochondrion; n, nucleus; s, sacs. At the lowest end is the free flagellum

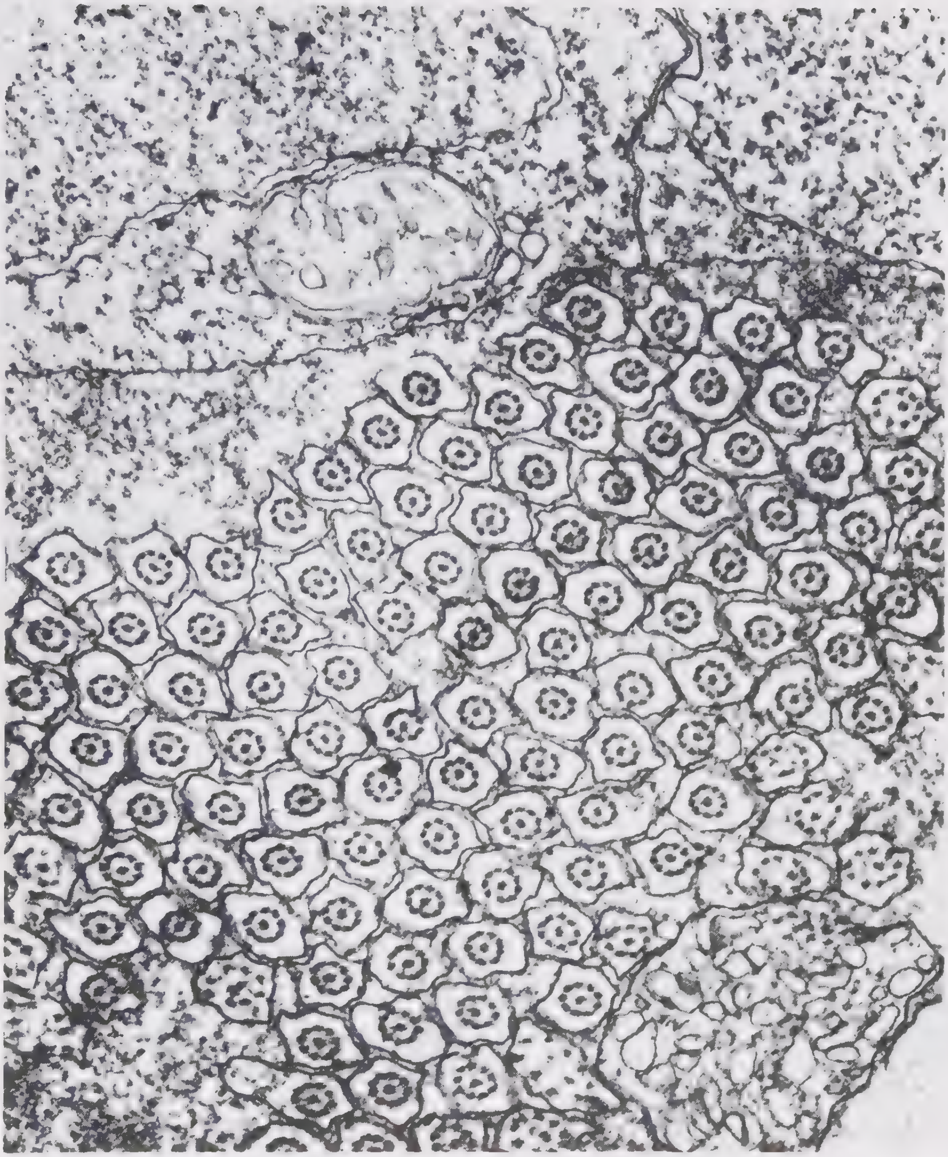

Fig. 4. A section through testis and neighbouring tissues of *S. euneritica*. Note the arrangement of the axoneme of the spermatozoa (×24,800). (Courtesy: Dr. Bernhard E. F. Reimann)

and here the complete double membrane ring of the cap is present. In the rest of the cap, the membrane has an opening where the outer and inner cap membranes are connected. The beaded structure in the cap region is flat with outer and inner membranes, and lies dorsally displaced to one side of the

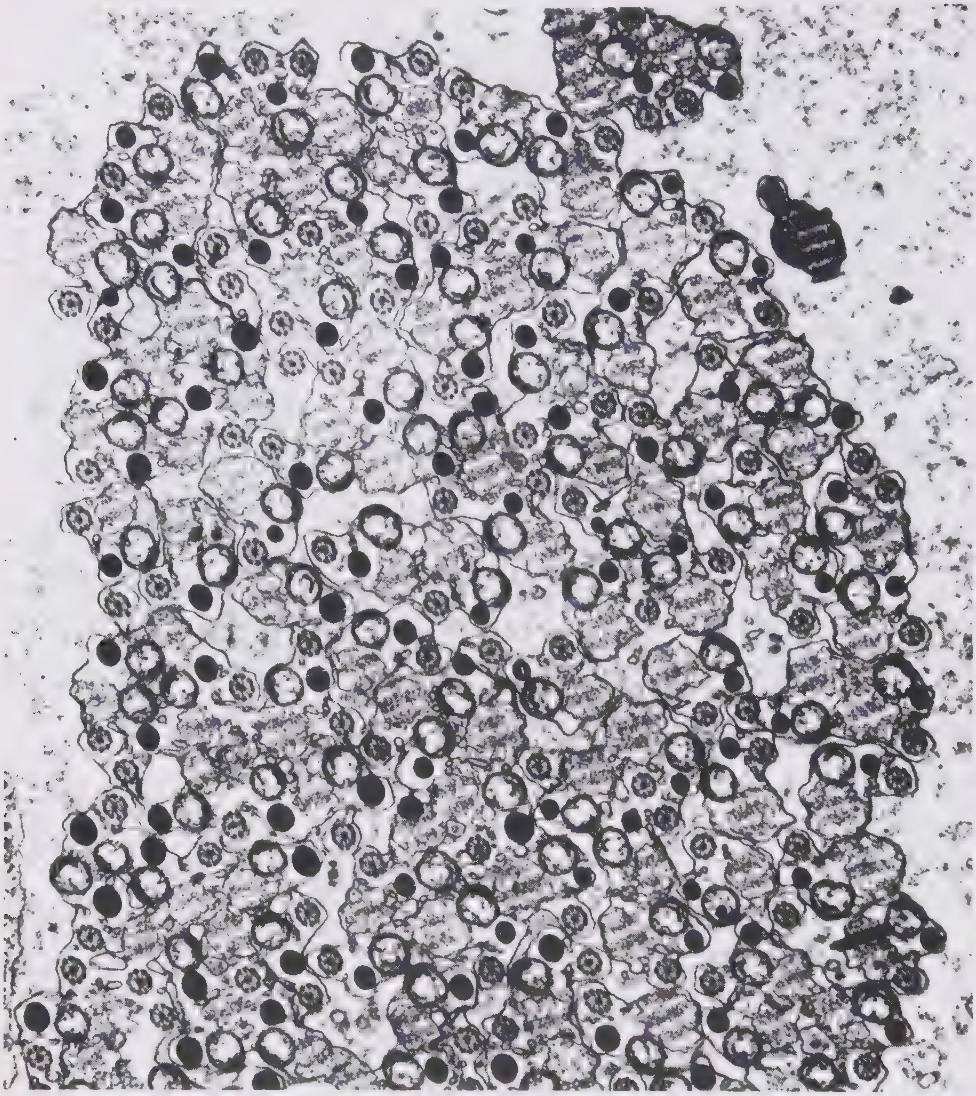

Fig. 5. A section through testis and neighbouring tissues of *S. euneritica*. The spermatozoa have been sectioned through nucleus, membrane cap, mitochondrion, etc. (×19,200). (Courtesy: Dr. Bernhard E. F. Reimann)

spermatozoon. The beaded structure at the dorsal part of the spermatozoon consists of a series of vesicles or sacs of rectangular or elliptical shape. Each sac is 0.8–1.4 µm long, 0.4 µm wide, and 0.2 µm high. Distance between sacs is small, and sometimes several sacs may merge together. Both cap membranes may be continuous with the sac membrane, although this is not very clear in mature spermatozoa. The nucleus of mature spermatozoon is at the posterior dorsal end of the axoneme. The nucleus appears as a dense rod, 60 μm long and 0.25 μm in diameter at the centre, tapering at both ends. The nuclear region overlaps in part the longitudinal sac region.

The mitochondrion is bilaterally symmetrical in structure, but not all along the spermatozoon, as it turns around the longitudinal axis with some lateral displacement. The two longitudinal sacs are 0.03 × 0.15 × 1.5 μm, situated between the mitochondrion and axoneme; or there may be two sacs on one side and one on the other. The transition from beaded sacs to longitudinal sacs is probably a gradual one. Axoneme (Fig. 4) extends from the front end of the spermatozoon, parallel to the mitochondrion surrounded by the membrane cap, and ends in a free flagellum (Fig. 3). Similarities are found between the spermatozoa of *Spadella* and *Sagitta*, and van Deurs (1972) indicates that a distinct acrosomal structure is not present in the spermatozoon of *Spadella*, but the membrane cap at the anterior end of the spermatozoon could be considered an acrosome. The mitochondrion and axoneme run parallel through almost the complete length of the spermatozoon (van Deurs, 1972). The ripe filiform spermatozoa move along the vas deferens from the testes, to be stored in the seminal vesicles.

V. SPERM STORAGE: SEMINAL VESICLES

Spectacular taxonomic differences exist in morphology of the seminal vesicles of the Chaetognatha (Tokioka, 1939; Alvariño, 1963, 1965, 1967, 1969). This may be because seminal vesicles need to be different in each species to avoid interspecific cross fertilization (Table 1). A detailed analysis of the structure of the opening of the oviducts would show that for each species oviducal openings and the devices of the seminal vesicles adapt and adjust conveniently. Also, the distance of the opening of the oviduct to the seminal vesicles is particular to each species, and this meristic factor is specific, and of primary importance to ensure copulation. The seminal vesicles are located laterally in the caudal portion of the body, just anterior to the caudal fin (Fig. 6). They are clothed by a layer of epidermis and lined with a layer of small gland cells, which probably produce a mucous substance.

The seminal vesicles of mature arrow-worms are tightly packed with filiform spermatozoa. The method of sperm emission is by rupture of the seminal vesicles by a slit or pore. Spermatophore formation has been mentioned by Dallot (1967), Ghirardelli (1968), and Nagasawa and Marumo (1978). I have observed extrusion of spermatozoa in *Sagitta enflata, Sagitta euneritica*, and other species; no formation of spermatophore was accomplished. Also, I have seen many hundreds of thousands of specimens of chaetognaths alive and preserved, from all the world oceans, but I have never found spermatophores. Although the chaetognaths are hermaphrodites, cross-fertilization is usual and obligatory. The semen is introduced by copulation into the receptaculum

Table 1
Chaetognatha: seminal vesicles (most common pelagic species)

Species	Seminal vesicles
Eukrohnia bathyantarctica	ovoid, opening at lateral dorsal side
E. bathypelagica	ovoid, opening at lateral dorsal side
E. fowleri	ovoid, opening at dorsal edge of the anterior part
E. hamata	ovoid, elongated, opening at dorsal edge of the anterior part
E. minuta	ovoid, elongated, opening at dorsal edge of the anterior part
Krohnitta mutabbii	oval, longer than in *K. pacifica*, touching both lateral and tail fins
K. pacifica	pear-shaped, oval, opening at top and dorsolaterally; fins cover them at the ventral side
K. subtilis	elongated oval; open at the anterolateral edge of dorsal side
Pterosagitta draco	elongated, oval, anterior part rounded; open dorsally at the anterolateral region
Sagitta gazellae	roundish, oval, opening at midlength of dorsal edge
S. lyra	oval, breaking at midlength of dorsolateral side
S. scrippsae	roundish, oval; open at midlength of dorsolateral side
S. maxima	oval, opening at midlength of dorsal side
S. hexaptera	small, spherical; rupture takes place at midlength over dorsolateral border
S. enflata	spherical, small, bursting by a fissure at the anterolateral edge along the dorsal side
S. pulchra	include two parts, an oval part and a spherical top, and open at the anterolateral dorsal side
S. bierii	pear-shaped, one prominence at top of anterior end, bending towards dorsal side; breaking by a pore at the base of the prominence.
S. pacifica	conspicuous with chitinous teeth at the anterolateral ventral side; a shield covers the anterior part, a device to ensure copulation. Bursting occurs at the anterodorsal side; the plate with the teeth opens like a lid leaving exposed a hole in the vesicle.
S. pseudoserratodentata	triangular, with prominence at lateral anterior corner, and small teeth or chitinous indentations at anterior end; open at anterior end of dorsal side
S. serratodentata	two prominences or horns at anterior lateral corner, opening at anterodorsal side
S. tasmanica	oval, with top formed by soft abundant papillae, a cap or lid covering the opening; the cap adapts to female openings, if evident
S. bombayensis	pear-shaped, anterior part large, opening at anterolateral dorsal edge
S. bruuni	oval, anterior part enlarged, opening out by anterodorsal fissure.

S. crassa	oval, with a roundish swelling at anterolateral end
S. euneritica	oval, with a roundish body at anterior part
S. euxina	oval, with roundish body at anterior part
S. friderici	oval, with a large posterior receptacle and a roundish anterior part
S. peruviana	oval, with posterior receptacle and roundish anterior part, opening at anterodorsal side
S. popovicii	oval, with a prominence at anterolateral side
S. setosa	oval, inconspicuous
S. tenuis	oval and elongated, with a swelling at anterior end; open by a latero-anterior fissure at dorsal side
S. bipunctata	pear-shaped, anterior part globular, opening at the anterodorsal side
S. macrocephala	oval, opening along a fissure extending at the dorsal outer edge
S. helenae	oval, with enlarged anterior part, opening at anterodorsal end
S. marri	conical, bursting at midlength of the dorsal edge
S. planctonis	oval, breaking at edge of dorsal side
S. zetesios	oval, open by a ridge along the dorsal side edge
S. bedoti	ovoid, with small prominence at anterolateral region; burst along the lateral edge by a fission line which extends from anterior end to the posterior part of the vesicle
S. nagae	oval with small prominence at the anterior part; open by a slit along the dorsolateral side; on the ventral side of the vesicle appears a triangular thin shield partially covering the vesicle.
S. elegans	conical; open at laterodorsal side
S. minima	oval, elongated, anterior part larger than the posterior; opening extends along dorsolateral side
S. decipiens	pear-shaped with the widest part at anterior end; a prominence or small shield at the ventral side
S. ferox	oval with a cup-like extension at the anterior end; they have two parts, an oval posterior section and an anterior section, covered by a shield like the shell of a bivalve mollusc; shield is of glandular and protective function
S. hispida	oval with hemispherical protuberance at anterior end; opening by a fissure extending along the dorsal edge
S. robusta	pear-shaped, anterior part roundish; opening at anterodorsal side
S. tokiokai	large oval with strong walls; opening is covered by a shield like the bivalve shell; the concave part of the shield lies against the opening of the spermatic sac and is lined with papillae
S. neglecta	oval, elongated, anterior part larger than the posterior; open along edge of dorsal side

Table 1 (continued)

Species	Seminal vesicles
S. regularis	elongated, oval; anterior part larger than the posterior; open along edge of dorsal side
S. bedfordii	pear-shaped; opening at anterolateral end of the dorsal side
S. johorensis	oval, almost spherical with a rounded prominence like a shield at anterolateral end, protecting the opening of the vesicle. At the anterior ventral side, a hard structure extends from the tail to the vesicle
S. oceania	pear-shaped with opening at the anterolateral part of dorsal side; a flap protects the opening ensuring copulation
S. septata	roundish oval, with a roundish extension at the anterior end; they open at the edge of dorsal side, and the line of rupture is well marked on the vesicle; a fine membrane extends from posterior end of the vesicle to base of the tail, holding the vesicles.

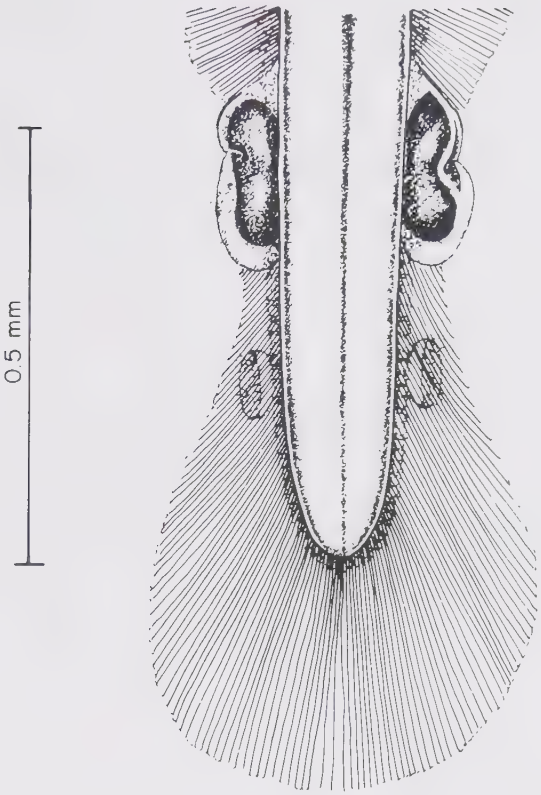

Fig. 6. Seminal vesicles of *Spadella gaetanoi* (a benthic chaetognath), dorsal view

seminis (annex to the ovary), each mating partner acting as a functional male and female.

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THE DEPTH DISTRIBUTION, RELATIVE ABUNDANCE AND STRUCTURE OF THE POPULATION OF THE CHAETOGNATHA *SAGITTA SCRIPPSAE* ALVARIÑO 1962, IN THE CALIFORNIA CURRENT OFF CALIFORNIA AND BAJA CALIFORNIA [*]

Ángeles Alvariño [**]

ABSTRACT

Sagitta scrippsae is an inhabitant of the Transition region of the North Pacific, occurring between 25 m and 475 m depth (but occasionally deeper) off California and Baja California. It is abundant in the strata between 100 and 350 m, decreasing gradually in numbers and area occupied above and below those layers.

The collections analyzed in this paper were obtained in 1969 off California and Baja California, from day and night hauls at identical locations and depth strata (0-25, 25-50, 50-75, 75-100, 100-225, 225-350, 350-475, 475-600m depth) on winter (February-March), spring (May-June), summer (August-September), and fall (November-December) cruises.

The greatest number of specimens was collected on the August-September cruise; the number was about twice that of November-December cruise, and three times that of the spring (May-June) cruise. The lowest number occurred in winter (February-March).

Sagitta scrippsae occurred off California and Baja California in waters deeper and farthest west and south in August-September than during any other season of 1969. It was present in the 25-0 m stratum only in February-March 1969.

Saggitta scrippsae was most abundant on the northern Line of Stations in each season, and less abundant or absent on the southernmost Lines. This distributional pattern indicates the source of the California population of *S. scrippsae* is in the waters north of California.

Present data indicate that *S. scrippsae* breeds in every season, with a peak in the summer and a low in winter. The life history of the species is analyzed, and the four Stages of maturity are described. Size ranges of each Stage are indicated, together with day and night distribution with respect to depth, location and season. Fluctuations in the size range of fully mature individuals are discussed.

The distribution of *S. scrippsae* off California and Baja California shows a positive correlation with the intensity of the California Current, gradually decreasing in numbers as the California Current losses its distinctiveness. Therefore, the species could be used as an indicator of the northern flow off California and Baja California to identify the farthest extent of these waters from the north, and to estimate the degree of mixing taking place in the California Current System. Evidence is outlined on the distribution of this chaetognath and the characteristics of some endemic and seasonal fisheries in this region.

RESUMEN

Sagitta scrippsae habita la región de Transición del Pacífico septentrional, principalmente en los 25 a 475 m de profundidad, pero puede aparecer a niveles más abisales frente a California y Baja California. Su mayor abundancia se ha observado entre los 100 y los 350 m de profundidad, decreciendo gradualmente en número de individuos

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[**] National Marine Fisheries Service Fishery-Oceanography Center, La Jolla, California 92037, USA.

y en espacio habitado, en los niveles por encima de los 100 m y por debajo de los 350 m de profundidad.

El material de plancton estudiado se obtuvo en las cuatro estaciones del año 1969 en aguas de California y Baja California, efectuando arrastres diurnos y nocturnos en todos los niveles batimétricos correspondientes a cada localidad. Los arrastres, con redes Bongo de apertura y cierre automáticos, ocuparon los niveles batimétricos de 0-25, 25-50, 50-75, 75-100, 100-225, 225-350, 350-475, 475-600 m, durante los cruceros de invierno (febrero-marzo), primavera (mayo-junio), verano (agosto-septiembre), otoño (noviembre-diciembre).

Sagitta scrippsae aparecía con mayor abundancia en el período de agosto-septiembre, resultando así estas poblaciones de magnitud doble a las obtenidas en el período de noviembre-diciembre y triplicando las correspondientes a la primavera; mientras que las poblaciones de invierno resultaron de escasa magnitud.

Las poblaciones de *S. scrippsae* frente a California y Baja California se extendían más hacia el oeste, el sur y niveles batimétricos más profundos durante el período de agosto-septiembre, que en las demás estaciones del año. Esta especie se observó en el estrato de 0-25 m de profundidad, solamente durante el invierno (febrero-marzo).

Sagitta scrippsae aparecía más abundante en todas las épocas del año en la enfilación de Estaciones de la parte más nórdica de la zona explorada, frente a California, y era menos abundante o estaba ausente de las Estaciones más meridionales, frente a Baja California. El patrón de la distribución de este organismo indica que las poblaciones que aparecen en aguas de California y Baja California proceden de zonas al norte de esa región.

Los datos que se han obtenido señalan que *S. scrippsae* se reproduce en todas las estaciones del año, con un máximo en verano y un mínimo en invierno. Se ha analizado el ciclo de vida de esta especie y se describen las cuatro fases de madurez sexual, indicando las tallas correspondientes a cada fase, así como la distribución diurna y nocturna para cada estación del año, en relación con el nivel batimétrico y la localidad. Se discuten las fluctuaciones en las tallas que presentan los individuos plenamente maduros.

La distribución de *S. scrippsae* frente a California y Baja California presenta una correlación positiva con la intensidad de la Corriente de California, disminuyendo progresivamente a medida que la Corriente va perdiendo su identidad. Por lo tanto, esta especie podría utilizarse como indicadora de la corriente nórdica que avanza frente a California y Baja California, para identificar la extensión abarcada por esas aguas procedentes del norte, y estimar la intensidad de la corriente y grado de mezcla que se produce en el Sistema de la Corriente de California. Se señala además la relación evidente entre la distribución de este Quetognato y las características que presentan algunas de las pesquerías endémicas y de temporada, en esta región.

INTRODUCTION

The areal distribution of the Chaetognatha in the California Current region is well known (Alvariño 1964, 1965a, 1966), but their life histories, depth distribution, and their role or function in the biological community in relation to the various confluent water masses in this region has not been thoroughly analyzed.

Sagitta scrippsae appears to be restricted to the Transition region (Alvariño 1962, 1964, 1965b; Kotori 1972), between the Subarctic and Pacific waters, from about 35°N to about 49°N and from 160°E to 140°W (Eber 1971). It extends into the Gulf of Alaska via de Alaska Gyre, and southward off North America via the California Current. *S. scrippsae* is also carried by eddies from the Transition region into the Central Pacific waters north of Hawaii (author's unpublished data). A few stray specimens have been obtained in the Pacific Subarctic waters, but none were found in the Bering Sea collections analyzed by Kitou (1976) and Kotori (1972). Two specimens of *S. scrippsae* were observed (Kotori and Hara 1972) at 54°00′N, 172°00′W in the Bering Sea: one from

325 m deep and another from 669 m. Kotori (1967) also found this species from 0 m to 560 m depth at locations (39°53′N to 49°58′N and 154°29′W to 155°24′W) in the Transition region, with highest abundance between 56 m, and 88 m depth.

The distribution of *S. scrippsae* off California appears to fluctuate with the strength of both the West Wind Drift in the Transition zone, and the California Current. It is most abundant at the northern end of the California Current, gradually decreasing in numbers as the Current flows southward (Alvariño 1962, 1964, 1965a, 1966). The abundance of this species could therefore be useful in identifying the influence of the northern waters as they extend southward off California and Baja California, and their various degrees of mixing with other waters of the California Current System.

The objectives of this study were to analyze the vertical and horizontal distribution of *S. scrippsae* Alvariño 1962, and to evaluate this species as an indicator of the northern flow into the California region. Fluctuations of numbers, the areas occupied, and the structure of the populations were studied to determine key locations and times at which the distribution pattern of *S. scrippsae* populations would indicate biotic and abiotic characteristics of the northern flow off California in spring and summer. This information may prove useful in studing the survival of California endemic fish larvae and the status of some seasonal fisheries in this region.

METHODS

The plankton collections used for analysis in this study were obtainer in 1969 during the following four seasonal cruises: 6902-03 (February-March), 6905-06 (May-June), 6908-09 (August-September), and 6911-12 (November-December). The Stations at which the samples were obtained correspond to Station Lines 70, 90, and 120 of the cruise pattern regularly occupied by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) off the west coasts of California (United States), and Baja California (México). The vertical distribution series occupied eleven Stations in those three Lines: Stations 70.60, 70.75, 70.90, and 70.110 on Line 70; Stations 90.45, 90.60, and 90.90 on Line 90; and Stations 120.45, 120.55, 120.70, and 120.90 on Line 120.

Specimens of *Sagitta scrippsae* were identified and enumerated from the whole of each sample (no aliquots were made). Each specimen was measured in millimeters, from the anterior end of the head to the end of the tail segment, excluding tail fin, and the Stage of maturity was determined.

Opening-closing Bongo nets (paired nets set side-by side) were used, with paired covers that, when closed, resemble a bongo drum. The nets in each set are labelled left (port) and right (starboard). These nets were towed at the same depth at each Station during both the day (near noon) and the night (near midnight). Thus, about 12 hours elapsed between the daylight and night hauls, giving the opportunity to evaluate day/night differences in vertical distribution. The Bongo nets take paired hauls at depth sampled. Therefore, 16 samples were expected from each day or night series, or 32 daily samples from each Station. A total of 352 samples were expected from each cruise (176 pairs). Due to irregular sampling on cruise 6902-03, however, only 188 samples were taken, resulting in a lower overall total.

During cruises 6905-06, 6908-09, and 6911-12, sampling was conducted in day and night hauls at four 125 m strata from 600 to 100 m (600 to 475 m, 475 to 350 m, 350 to 225 m, and 225 to 100 m), and at four 25 m strata from 100 m to the surface (100 to 75 m, 75 to 50 m, 50 to 25 m, and 25 to 0 m). The depths sampled in cruise 6902-03, however, were shallower than in the other cruises, and often covered differently spaced strata. Three depths, 350-225 m, 475-350 m, and 600-475 m were not sampled, and sampling within the upper 225 m was variable. Therefore, cruise 6902-03 data are not strictly comparable to those from other cruises, although the uneven hauls in the upper 225 m for this cruise could be compared to combined adjacent strata from other cruises.

Net mesh size also varied from cruise to cruise:

On cruise 6902-03, the net mesh was NITEX 333 cod end NITEX 223 (sometimes NITEX 102). On cruise 6905-06, net mesh was 505 cod end 333, or net mesh 333 cod end 223 for the pair. On cruises 6908-09 and 6011-12, net mesh was 333 cod end 223. Changes in mesh size used in the net and cod end probably accounted, is some instances, for certain variations in the numbers and sizes of the specimens collected.

Flow meters were used to close the nets when the combined volume of water strained by the two nets at each sampled stratum equally 1000 m^3. The amount of water filtered per meter depth, however, was not identical for each stratum sampled. In the shallow hauls that sampled a 25 m depth stratum, for example, the amount of water filtered per meter of depth fished was 40 m^3, whereas in the deeper hauls that sampled the 125 m depth stratum, the amount of water filtered per meter of depth fished was only 8 m^3. To obtain the water-column abundance of *S. scrippsae*, the counts were standardized to equivalent volumes of water strained for each meter of depth fished for each depth stratum. For simplicity in comparing the abundance in the upper net hauls (numbers per 1000 m^3 across 25 m depth), the values selected represented the number under 40 square meters of sea surface (i.e. the sum of the numbers in 40 m^3 per each meter of depth sampled, throughout the 600 m depth strata). It was determined that, in order to obtain the same volume of water strained by the nets in both the shallow and deep water series the time spent per meter of depth in the sampling for a 25 m stratum was five times that for a 125 m stratum.

A standardization was therefore necessary to obtain quantitatively comparable data for the strata in the upper 100 m and the strata below this depth (Kramer and Ahlstrom 1968). The counts were standardized to 1000 m^3 of water for each 25 m depth (number beneath 40 m^2) by the formula,

$$N = n\,\frac{(\text{opening depth-closing depth})}{25}$$

N = Standardized number of specimens

n = Number of specimens, for port (left) and starboard (right) Bongo nets combined.

If the sample from either net (port or starboard) in any haul was missing, it was estimated that an equal number of specimens would have been obtained in the missing haul if it had functioned properly. Therefore, the values of the good available sample, port or starboard, were simply doubled. Wen it was evident, either from the sample or from direct observation on shipboard, that the net did not function properly and sampled other than the intended depth, the data were not used. The information in the results corresponds only to the nets working properly (that is, opening and closing at the right depth layer). If a haul was not made, there is no way to interpolate the amount of individuals present at the location and time.

A total of 704 hauls was made with the paired Bongo nets, equal to 1408 expected samples. The total number of actual samples taken corresponds to 440 hauls with both nets working (880 samples), plus 59 hauls with only one net working: a total of 939 samples.

On the comparable cruises 6905-06, 6908-09, and 6911-12, there were Stations that were completely missed, either during the daylight or night series. The most complete set of collections corresponds to cruise 6905-06, and the least complete to 6902-03. Less than 38% of the data are missing or incomplete. In all, 438 of 608 levels of sampling attempted were successful, in that at least one of the two nets appeared to have functioned.

The following series of hauls did not appear in the collections: Day series at Station 90.45 of cruise 6905-06, night series at Station 70.60 of cruise 6908-09, night series at Station 70.75, and both day and night series at Stations 70.90 and 70.110 of cruise 6911-12.

Malfunctions involving both nets at a given depth occurred for 10 pairs during 6902-03, 20 pairs for 6905-06, 28 pairs for 6908-09, and 22 pairs of 6911-12 (total, 80 pairs of hauls).

Gear malfunction involving only one net of the pair occurred for 6 depth strata for 6902-03, 9 depth strata for 6905-06, 27 depth strata for 6908-09, and 17 depth strata for 6911-12, resulting in a total of 59 depth strata.

These results are sumarized below:

Cruise	Sample lost due to non-occupancy	2 nets mal functioned	1 net mal functioned	Both hauls apparently working	Total
6902-03	69	10	6	91	176
6905-06	8	20	9	139	176
6908-09	8	28	27	113	176
6911-12	40	22	17	97	176
	125	80	59	440	704
%:	17.7	11.4	8.4	62.5	100

It is important to note that most of the missed Stations and gear malfunctions occurred on Line 70, the most valuable location for determination of the *Sagitta scrippsae* entering the California region:

Line 70	No sample either net	Sample in I net of pair	Samples in both nets	Total
6902-03	48	3	13	64
6905-06	5	5	54	64
6908-09	29	8	27	64
6911-12	41	6	17	64
Total:	123	22	111	256
%:	48.0	8.6	43.4	100

In addition, the deepest net seldom sampled below 300 m during 6902-03 cruise, so data are lacking for the deep strata during February and March 1969. Net failures were responsible for the occasional lack of samples from intermediate levels within series. These gaps complicate the analyses of the material because of the attendant difficulties in presenting well defined vertical distribution patterns of the species.

SEASONAL AND DIURNAL VARIATION IN THE BATHYMETRIC DISTRIBUTION OF THE SPECIES

The geographical and bathymetric distribution of *S. scrippsae* off California and Baja California is shown in Figures 1, 2, 3, and 4 for day and night sampling at each of the Stations on CalCOFI Lines 70, 90, and 120 for the four seasons of 1969. In addition, basic counts of abundance-per-1000 m^3 of the different sizes of *S. scroppsae* (Table A) were averaged using values determined for each 25 m depth interval from 600 m to 0 m for each season (Tables B, C, D, E, and F).

FEBRUARY-MARCH 1969 CRUISE (6902-03).
Figure 1.

Line 70. Two Stations were occupied with more daylight than night hauls. At Station

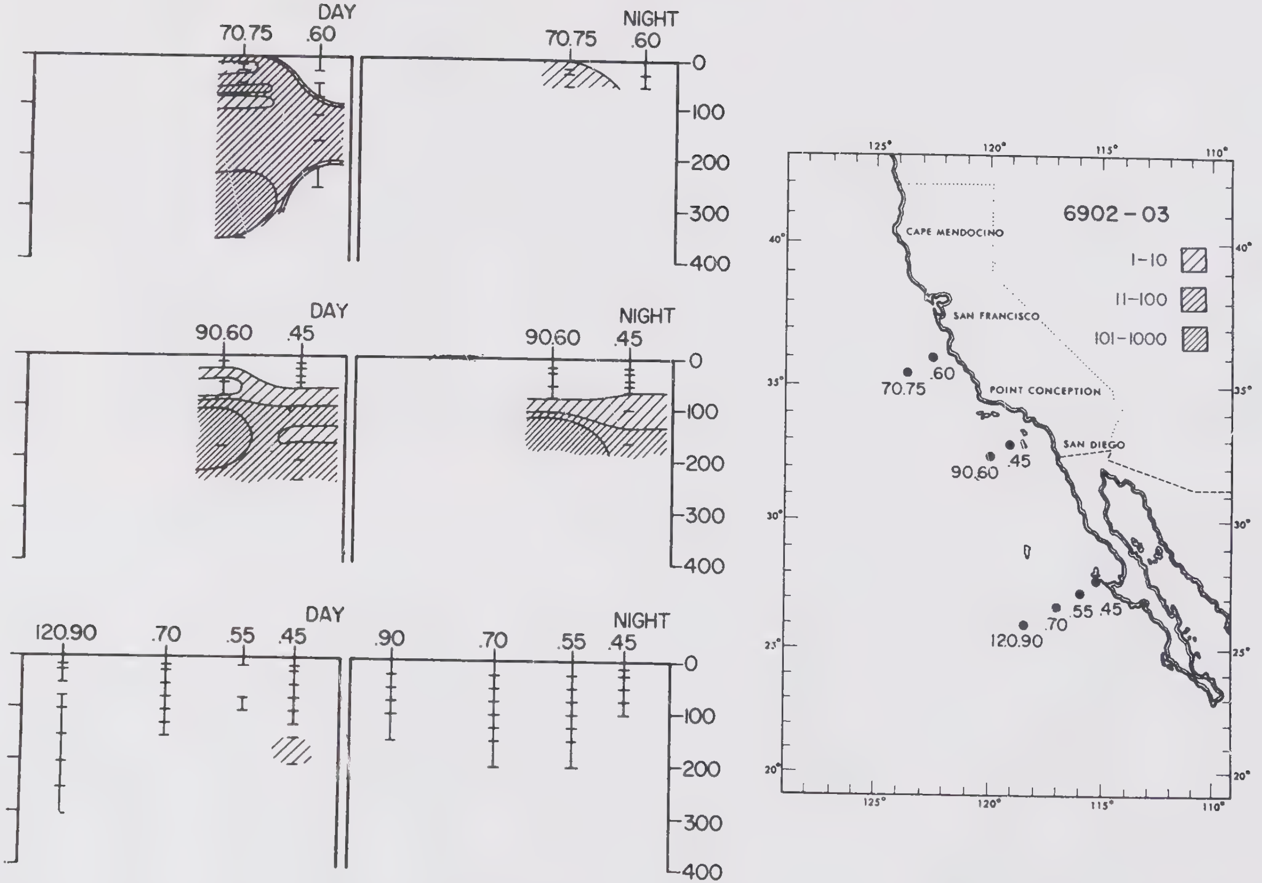

Fig. 1. Vertical days and night distribution of *S. scrippsae* on Lines 70, 90, 120, off California and Baja California, February-March, 1969 (6903.03). Vertical lines indicate hauls were taken and the species was absent.

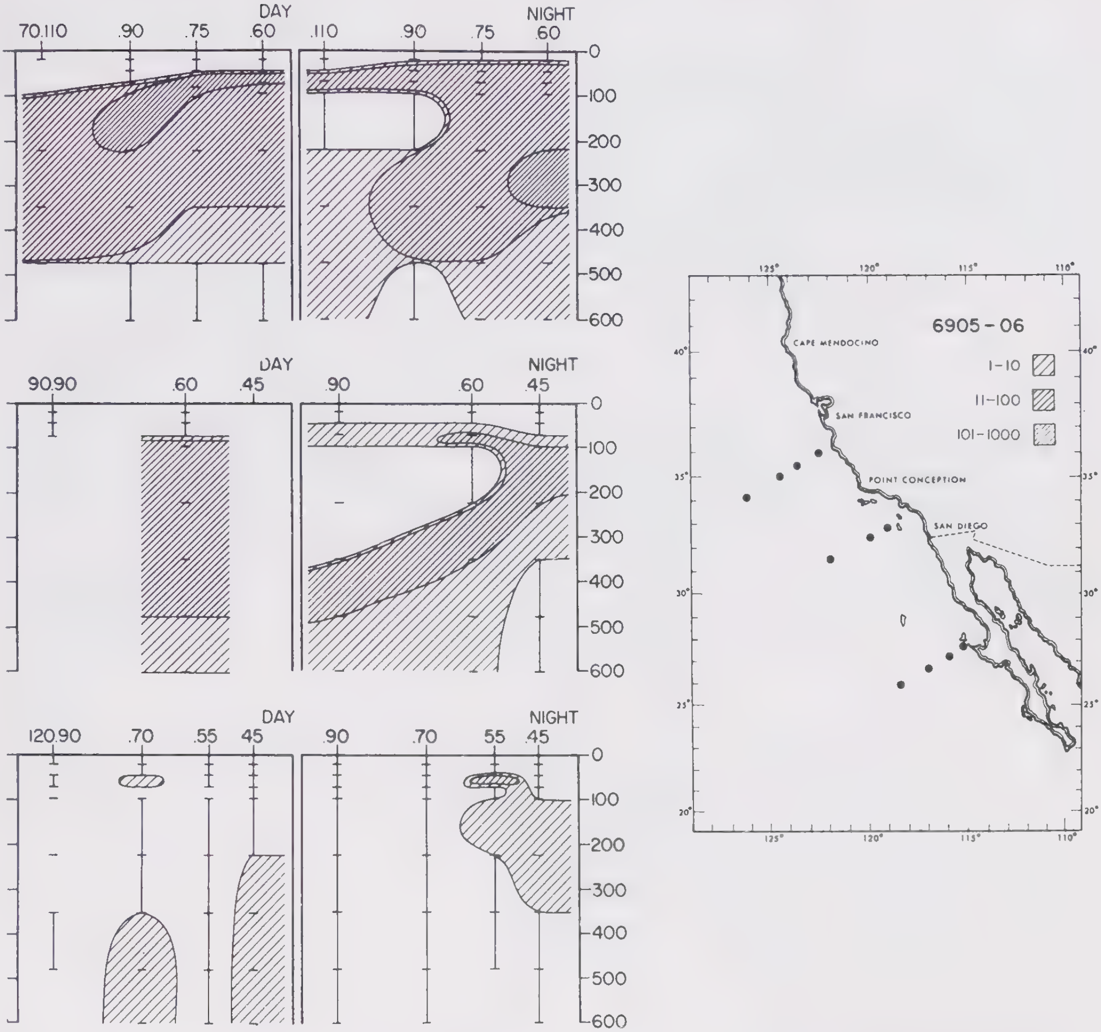

Fig. 2. Vertical day and night distribution of *S. scrippsae* on Lines 70, 90, 120, off California and Baja California, May-June, 1969 (6905-06). Vertical lines indicate hauls were taken and the species was absent.

70.60, daylight hauls were made at seven depth strata, from 0 to 256 m in depth, and specimens were taken between depths of 208 to 75 m. No sample was obtained from the 50-25 m depth, and no *S. scrippsae* were collected at the 250-200 m depth. At Station 70.75, hauls were also made at seven depths, 0 to 350 m, and specimens were taken at all depths except 25-15 m. The highest concentrations were at 75-50 m and 350-225 m, and next highest at three other strata (225-100 m, 50-25 m, and 15-0 m); the lowest (less than 10 speciments) occurred at 100-75 m. Night hauls were obtained only in shallow depths (50-0 m). Few specimens were obtained at Station 70.75.

Line 90. Two Stations, 90.45 and 90.60, were occupied. Most hauls were taken during daylight. During the day, 10 depths were sampled from 240 to 0 m at Station 90.45. *Sagitta scrippsae* was absent both day and night in the upper

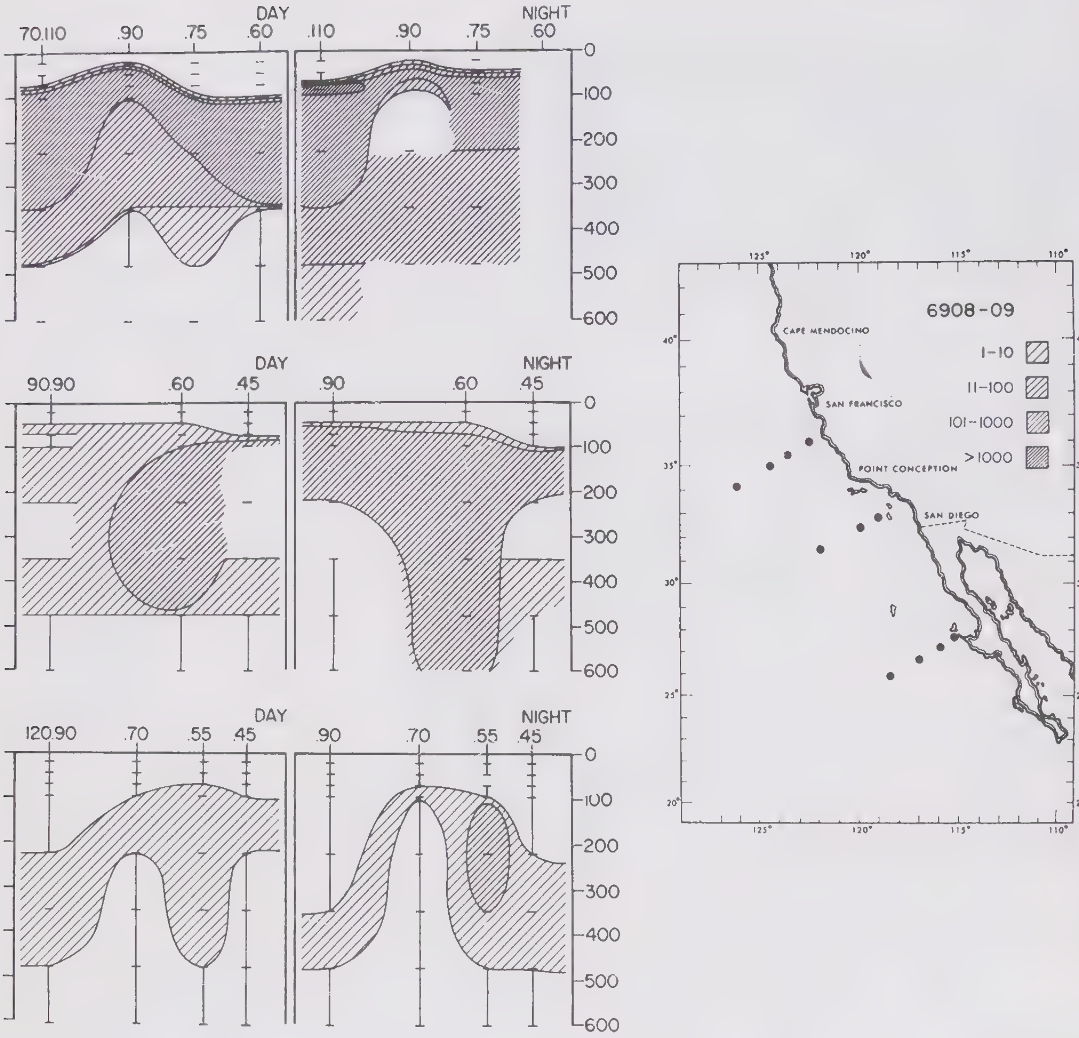

Fig. 3. Vertical day and night distribution of *S. scrippsae* on Lines 70, 90, 120, off California and Baja California, August-September, 1969 (6908-09). Vertical lines indicate hauls were taken and the species was absent.

hauls (levels in the 100-0 m strata), primarily from 60 to 0 m. Moderate numbers (11 to 100 specimens per 1000 m^3) of *S. scrippsae* were collected during daylight at 240-168 m and 130-95 m depths, and at night at 168-130 m depth. Fewer than 10 specimens were obtained at other strata. At Station 90.60, eight hauls were made in daylight (213 to 0 m), and seven hauls at night (176 to 0 m). *S. scrippsae* was not collected in daylight hauls at 22-0 m or 75-34 m, nor in five hauls made in the 75-0 m strata at night. The highest concentration of this species was obtained at 213-100 m (daylight) and at 176-100 m (night), with moderate concentration at 100-75 m (daylight); the lowest numbers occurred at 34-22 m (daylight) and 100-75 m (night).

Line 120. Although four Station on Line 120

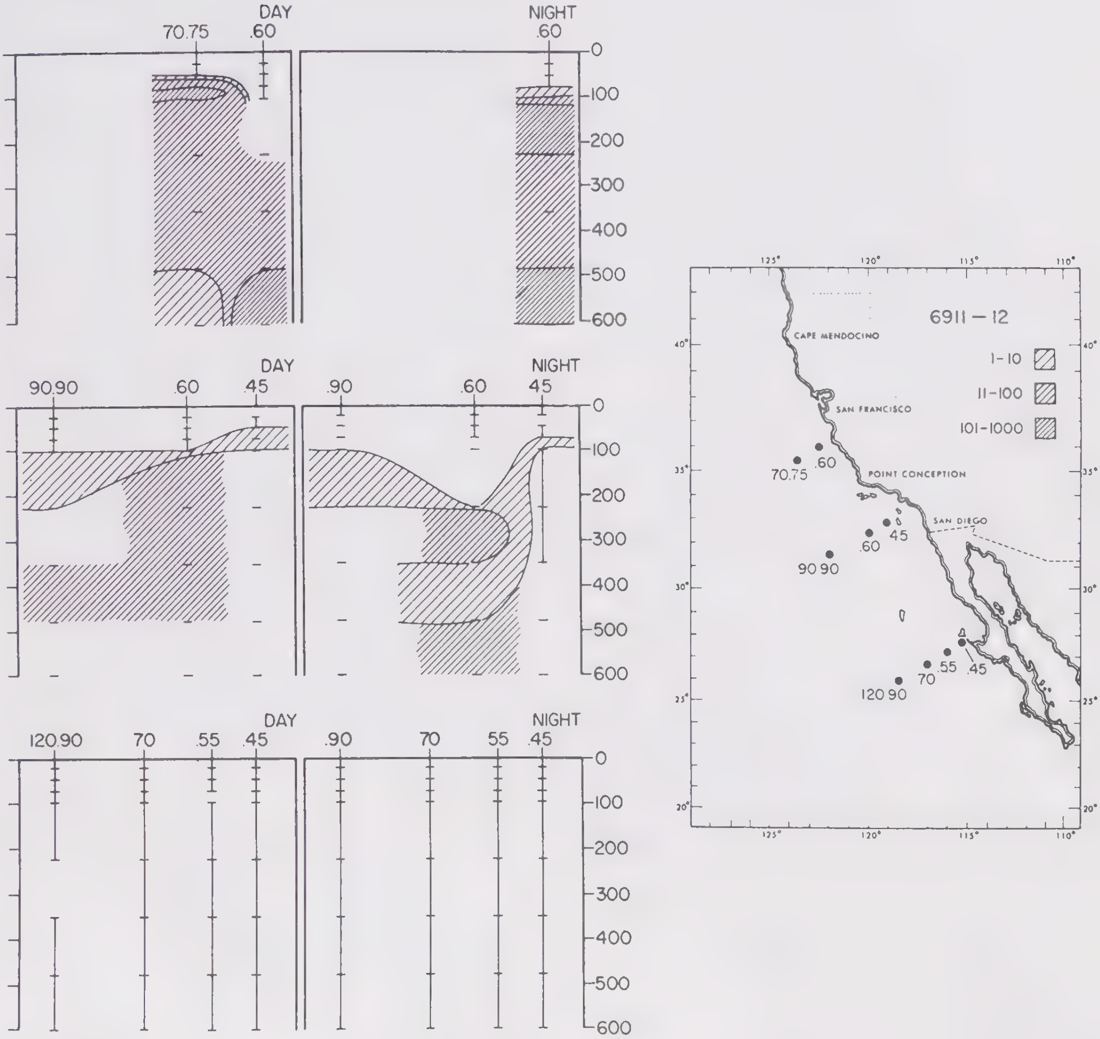

Fig. 4. Vertical day and night distribution of *S. scrippsae* on Lines 70, 90, 120, off California and Baja California, November-December, 1969 (6911-12). Vertical lines indicate hauls were taken and the species was absent.

were sampled at various depths, only one specimen was taken at Station 120.45 in a 200-150 m depth haul during daylight hours.

MAY-JUNE 1969 CRUISE (6905-06). Figure 2.

Line 70. All Stations were occupied both during the day and at night. Eight strata, from 600 to 0 m, were sampled at four Stations. Daylight samples were not obtained at 350-225 m at Station 70.60, nor at depths 50-25 m, 75-50 m, 100-75 m, or 600-475 m at Station 70.110. At Station 70.60, no *S. scrippsae* appeared in the upper two hauls (at 50-0 m layers), at 600-475 m during daylight, nor in the 25-0 m at night. During daylight, high numbers (more than 100 specimens per 1000

Table A

THE BASIC COUNTS OF *SAGITTA SCRIPPSAE*. STANDARIZED

Cruise Station	Depth m	DAY Original counts		Stand. total	NIGHT Original counts		Stand. total
		Port	Stbd .		Port	Stabd.	
6902-0.							
70.60	25-0	0	0	0	0	0	0
	50-25	-	-	-	0	0	0
	75 50	0	0	0	-	-	-
	112-75	33	-	98	-	-	-
	160-112	12	16	54	-	-	-
	208-160	46	-	184	-	-	-
	256-208	0	0	0	-	-	-
70.75	15-0	30	16	28	1	0	1
	25-15	0	0	0	1	-	1
	50-25	0	61	61	0	6	6
	75-50	233	380	613	-	-	-
	100-75	8	0	8	-	-	-
	225-100	11	18	145	-	-	-
	350-225	174	173	1735	-	-	-
90.45	15-0	0	0	0	0	0	0
	25-15	0	0	0	0	0	0
	40-25	0	0	0	0	0	0
	50-40	0	0	0	0	0	0
	60-50	0	0	0	0	0	0
	95-60	0	2	3	2	-	6
	130-95	10-	24	28	-	2	6
	168-130	1	-	3	0	16	24
	203-168	14	4	25	-	-	-
	240-203	14	10	36	-	-	-

Table A (Continuation)

Cruise Station	Depth m	DAY Original counts		Stand. total	NIGHT Original counts		Stand. total
		Port	Stabd.		Port	Stabd.	
6902-05							
70.60	11-0	0	0	0	0	0	0
	22-11	0	0	0	0	0	0
	34-22	1	0	1	0	0	0
	50-34	0	0	0	0	0	0
	100-75	31	0	31	1	1	2
	176-100	57	69	378	55	54	330
	213-176	105	85	285	-	-	-
120.45	15-0	0	0	0	0	0	0
	25-15	0	0	0	0	0	0
	50-25	0			0	0	0
	75-50	0	0	0	0	0	0
	100-75	0	0	0	0	0	0
	125-100	0	0	0	-	-	-
	150-125	-	-	-	-	-	-
	200-150	1	0	2	-	-	-
120.55	15-0	0	0	0	0	0	0
	25-15	-	-	-	0	0	0
	50-25	-	-	-	0	0	0
	75-50	-	-	-	0	0	0
	100-75	0	0	0	0	0	0
	125-100	-	-	-	0	0	0
	150-125	-	-	-	0	0	0
	200-150	-	-	-	0	0	0
120.70	15-0	0	0	0	0	0	0
	25-15	0	0	0	0	0	0
	50-25	0	0	0	0	0	0
	75-50	0	0	0	0	0	0
	100-75	0	0	0	0	0	0
	125-100	0	0	0	0	0	0
	150-125	0	0	0	0	0	0
	200-150	-	-	-	0	0	0

Table A (Continuation)

Cruise Station	Depth m	DAY Original counts		Stand. Total	NIGHT Original counts		Stand. total
		Port	Stabd.		Port	Stabd.	
6902-0							
120.90	15-0	0	0	0	0	0	0
	25-15	0	0	0	0	0	0
	50-25	0	0	0	0	0	0
	75-50	-	-	-	0	0	0
	100-75	0	0	0	0	0	0
	150-100	0	0	0	0	0	0
	200-150	0	0	0	-	-	-
	250-200	0	0	0	-	-	-
	300-250	0	0	0	-	-	-
6905-06							
70.60	25-0	0	0	0	0	0	0
	50-25	0	0	0	10	7	17
	75-50	10	136	146	14	4	18
	100-75	2	57	59	15	53	68
	225-100	19	-	190	28	34	310
	350-225	-	-	-	32	92	620
	475-350	3	3	30	2	-	20
	600-475	0	0	0	1	-	10
70.75	25-0	0	0	0	0	0	0
	50-25	0	0	0	12	14	26
	75-50	62	245	307	3	42	45
	100-75	157	76	233	30	50	80
	225-100	12	9	105	18	7	125
	350-225	24	19	215	36	48	420
	475-350	-	4	40	7	4	55
	600-475	0	0	0	2	8	40

Table A (Continuation)

Cruise Station	Depth m	DAY Original counts		Stand. total	NIGHT Original counts		Stand. total
		Port	Stbd.		Port	Stabd.	
6905-06							
70.90	25-0	0	0	0	0	0	0
	50-25	0	0	0	1	17	18
	75-50	0	0	0	10	1	11
	100-75	4	21	26	22	66	88
	225-100	66	71	685	0	0	0
	350-225	23	26	245	12	10	255
	475-350	26	42	340	29	16	225
	600-475	0	0	0	0	0	0
70.110	25-0	0	0	0	0	0	0
	50-25	-	-	-	0	0	0
	75-50	-	-	-	10	12	22
	100-75	-	-	-	-	10	20
	225-100	47	10	285	0	0	0
	350-225	5	8	65	5	5	50
	475-350	4	7	55	2	0	10
	600-475	-	-	-	1	0	5
90.45	25-0	-	-	-	0	0	0
	50-25	-	-	-	0	0	0
	75-50	-	-	-	0	0	0
	100-75	-	-	-	1	0	1
	225-100	-	-	-	10	4	70
	350-225	-	-	-	6	3	45
	475-350	-	-	-	0	0	0
	600-475	-	-	-	0	0	0
90.60	25-0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0
	75-50	0	0	0	0	2	4
	100-75	4	9	13	10	3	13
	225-100	9	11	100	0	0	0
	350-225	12	35	235	15	9	120
	475-350	7	9	80	2	0	10
	600-475	0	1	5	-	1	10

TABLE A (Continuation)

Cruise Station	Depth m	DAY Original counts		Stand. total	NIGHT Original counts		Stand. total
		Port	Stabd.		Port	Stabd.	
6905-06							
90,90	25-0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0
	75-50	0	0	0	2	0	2
	100-75	-	-	-	-	1	2
	225-100	-	-	-	-	-	-
	350-225	-	-	-	-	-	-
	475-350	-	-	-	9	19	140
	600-475	-	-	-	4	4	40
120,45	25-0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0
	75-50	0	0	0	0	0	0
	100-75	0	0	0	0	0	0
	225-100	0	0	0	1	0	5
	350-225	1	0	5	1	-	10
	475-350	1	2	15	0	0	0
	600-475	0	1	5	0	0	0
120,55	25-0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0
	75-50	0	0	0	17	0	17
	100-75	-	-	-	0	0	0
	225-100	0	0	0	1	0	5
	350-225	0	0	0	0	0	0
	475-350	0	0	0	0	0	0
	600-475	0	0	0	-	-	-
120,70	25-0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0
	75-50	1	0	1	0	0	0
	100-75	-	-	-	0	0	0
	225-100	0	0	0	0	0	0
	350-225	0	0	0	0	0	0
	475-350	0	1	5	0	0	0
	600-475	1	1	10	0	0	0

TABLE A (Continuation)

Cruise Station	Depth m	DAY Original counts		Stand. total	NIGHT Original counts		Stand. total
		Port	Stabd.		Port	Stabd.	
6905-06							
120,90	25-0	0	0	0	0	0	0
	50-25	-	-	-	0	0	0
	75-50	0	0	0	0	0	0
	100-75	-	-	-	0	0	0
	225-100	-	-	-	0	0	0
	350-225	-	-	-	0	0	0
	475-350	0	0	0	0	-	0
	600-475	-	-	-	0	0	0
6908-09							
70,60	25-0	-	-	-	-	-	-
	50-25	-	-	-	-	-	-
	75-50	-	-	-	-	-	-
	100-75	-	-	-	-	-	-
	225-100	90	59	745	-	-	-
	350-225	106	74	900	-	-	-
	475-350	0	0	0	-	-	-
	600-475	-	0	0	-	-	-
70,75	25-0	-	-	-	-	-	-
	50-25	-	-	-	-	-	-
	75-50	-	-	-	381	514	895
	100-75	-	-	-	-	87	174
	225-100	-	126	1260	205	216	2105
	350-225	12	28	200	7	74	405
	475-350	-	1	10	2	29	155
	600-475	-	-	-	-	-	-

TABLE A (Continuation)

Cruise Station	Depth m	DAY Original counts		Stand. total	NIGHT Original counts		Stand. total
		Port	Stabd.		Port	Stabd.	
6908-09							
70,90	25-0	-	-	-	-	-	-
	50-25	270	-	540	11	29	40
	75-50	130	285	415	78	38	116
	100-75	-	175	350	27	25	52
	225-100	14	6	100	-	-	-
	350-225	10	14	120	10	17	135
	475-350	0	0	0	11	5	30
	600-475	-	-	-	-	-	-
70,110	25-0	0	0	0	0	0	0
	50-25	-	-	-	-	-	-
	75-50	0	0	0	0	0	0
	100-75	-	189	378	-	798	1596
	225-100	86	68	770	447	218	3325
	350-225	69	32	505	67	69	680
	475-350	12	33	225	15	18	165
	600-475	-	-	-	-	5	5
90,45	25-0	0	0	0	0	0	0
	50-25	0	0	0	0	-	0
	75-50	0	0	0	0	0	0
	100-75	-	35	70	-	0	0
	225-100	-	-	-	9	34	215
	350-225	-	-	-	-	-	-
	475-350	1	1	10	0	1	5
	600-475	-	0	0	-	0	0
90,60	25-0	0	-	0	0	0	0
	50-25	0	0	0	0	0	0
	75-50	1	1	2	1	0	1
	100-75	1	4	5	0	24	24
	225-100	7	14	105	7	12	95
	350-225	27	25	260	15	3	90
	475-350	22	13	175	30	17	235
	600-475	-	0	0	6	-	60

TABLE A (Continuation)

Cruise Station	Depth m	DAY Original counts		Stand. total	NIGHT Original counts		Stand. total
		Port.	Stabd.		Port	Stabd.	
6908-09							
90,90	25-0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0
	75-50	4	2	6	7	5	12
	100-75	-	0	[illegible]	-	6	12
	225-100	8	0	[illegible]	12	13	125
	350-225	-	-	-	-	-	-
	475-350	[illegible]	1	5	[illegible]	0	0
	600-475	[illegible]	[illegible]	0	[illegible]	0	0
120,45	25-0	[illegible]	0	0	0	0	0
	50-25	0	0	0	0	0	0
	75-50	0	0	0	-	-	-
	100-75	[illegible]	[illegible]	5	0	0	0
	225-100	2	[illegible]	[illegible]	5	7	60
	350-225	1	[illegible]	[illegible]	[illegible]	11	70
	475-350	1	0	5	1	0	5
	600-475	0	0	0	0	0	0
120,55	25-0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0
	75-50	0	0	0	0	0	0
	100-75	0	0	0	1	-	2
	225-100	1	0	5	0	0	0
	350-225	0	[illegible]	0	0	0	0
	475-350	0	0	0	0	0	0
	600-475	0	0	0	0	0	0
120,70	25-0	0	0	0	0	0	0
	50-25	0	[illegible]	0	0	0	0
	75-50	[illegible]	0	[illegible]	0	0	0
	100-75	[illegible]	[illegible]	[illegible]	1	-	2
	225-100	1	[illegible]	[illegible]	0	0	0
	350-225	[illegible]	[illegible]	[illegible]	0	0	0
	475-350	[illegible]	0	0	0	0	0
	600-475	[illegible]	0	0	0	0	0

TABLE A (Continuation)

Cruise Station	Depth m	DAY Original counts Port	DAY Original counts Stbd.	Stand. total	NIGHT Original counts Port	NIGHT Original counts Stbd.	Stand. total
[illegible]							
[illegible]	25-0	0		0	0	0	0
	50-25	0	-	0	0	0	0
	75-50	-	[illegible]	0	0	0	0
	100-75	0		[illegible]	[illegible]	0	0
	225-100	0		[illegible]	-	0	0
	350-225	1		5		0	0
	475-350	1			1	0	5
	600-475	0	[illegible]		0	[illegible]	0
6911-12							
70.60	25-0	[illegible]		[illegible]		[illegible]	0
	50-25	0	[illegible]	0		0	0
	75-50	0	-		-		0
	100-75				[illegible]	-	3
	225-100	-	-	-	1	[illegible]	[illegible]
	350-225	4	[illegible]	[illegible]	[illegible]	11	105
	475-350	[illegible]	-	[illegible]	0	[illegible]	155
	600-475	-		[illegible]	13	187	1850
70.75	25-0	0		0	-	-	-
	50-25	0		0	-	-	-
	75-50	-	6	16	-	-	-
	100-75	[illegible]	[illegible]	[illegible]	-	-	-
	225-100	7	[illegible]	[illegible]	-	-	-
	350-225	3	[illegible]	[illegible]	-	-	-
	475-350	[illegible]	[illegible]	430	-	-	-
	600-475	1	0	5	-	-	-

TABLE A (Continuation)

Cruise Station	Depth m	DAY Original counts Port	DAY Original counts Stbd.	Stand. total	NIGHT Original counts Port	NIGHT Original counts Stbd.	Stand. total
[illegible]							
[illegible]	[illegible]	-	-	-		[illegible]	[illegible]
	[illegible]	-			-	-	-
	[illegible]						[illegible]
	[illegible]			1	-		[illegible]
	[illegible]	-	-	-	-		[illegible]
	[illegible]	-	-	-		-	
	[illegible]	-	-	-	-	-	-
	[illegible]	-	-	-	-	-	-
90.60	[illegible]		[illegible]	[illegible]			[illegible]
	[illegible]			[illegible]			[illegible]
	[illegible]						[illegible]
	[illegible]	[illegible]	-		-	-	-
	[illegible]		-		-		-
	[illegible]		[illegible]	1			1
	[illegible]			[illegible]		[illegible]	
	[illegible]	-	-	-	[illegible]		
[illegible]	[illegible]						
	[illegible]				-	-	-
	[illegible]				-	-	-
	[illegible]				-	-	-
	[illegible]				1		
	[illegible]	-	-	-	-	-	-
	[illegible]	11	1	[illegible]	-	-	-
	[illegible]	-		-	-	-	-
[illegible]	[illegible]						
	[illegible]						
	[illegible]						
	[illegible]						
	[illegible]					-	-
	[illegible]						
	[illegible]					[illegible]	[illegible]
	[illegible]	[illegible]		[illegible]	[illegible]	0	0

TABLE A (Continuation)

Cruise Station	Depth m	DAY Original counts Port	DAY Original counts Stbd.	Stand. total	NIGHT Original counts Port	NIGHT Original counts Stbd.	Stand. total
6911-12							
120.55	25-0	0	0	[illegible]	0	0	0
	50-25	-	0		0	0	0
	75-50	[illegible]	-	[illegible]	[illegible]	-	0
	100-75	-	-	-	0	0	0
	225-100				[illegible]	[illegible]	0
	350-225		0	[illegible]	0	[illegible]	0
	475-350	[illegible]			[illegible]	0	0
	600-475				[illegible]	[illegible]	0
[illegible]	25-0	[illegible]	[illegible]	[illegible]		[illegible]	0
	50-25		[illegible]	0	[illegible]	[illegible]	0
	75-50	[illegible]	[illegible]	[illegible]		[illegible]	0
	100-75	[illegible]					0
	225-100		[illegible]		[illegible]		0
	350-225		[illegible]				0
	475-350	[illegible]		[illegible]	[illegible]	[illegible]	0
	600-475	0	0	[illegible]	0	[illegible]	0
120.90	25-0	[illegible]	0	0	0	0	0
	50-25	0	0	0	0	[illegible]	0
	75-50	0	0	[illegible]	0	0	0
	100-75	0	[illegible]	0	0	0	0
	225-100	0	[illegible]	0	0	0	0
	350-225	-	-	-	0	0	0
	475-350	0			0	0	0
	600-475	0	0	0	0	0	0

m³ of water) were obtained at 75-50 m depth, and moderate numbers (11 to 100 specimens per 1000 m³ of water) at 225-100 m; few specimens (1 to 10) were obtained at 475-350 m depth. At night the highest concentration appeared at 350-225 m, with moderate numbers at 225-25 m; the lowest number occurred at 600-350 m depth.

At Station 70.75, *S. scrippsae* was absent in the upper two hauls (in strata 50-0 m), at 600-475 m during daylight, and at 25-0 m at night. The highest concentration during daylight was observed at 100-50 m, with moderate numbers at 350-100 m; the minimum was at 475-350 m. At night, moderate concentrations extended from 475 to 25 m, and the minimum occurred at 600-475 m depth.

At Station 70.90, the species was absent during daylight in the upper three hauls (at 75-0 m strata) and at 600-475 m depth, and at night in the 25-0 m, 225-100 m, and 600-475 m depth. The highest concentration during daylight occurred at 225-100 m, with moderate numbers at 475-225 m and 100-75 m depth. At night, moderate numbers were found at 100-25 m and 475-225 m depth.

At Station 70.110, *S. scrippsae* was absent in the uppermost hauls (in the 100-0 m strata) during daylight, and in the 50-0 m strata and 225-100 m at night. The species appeared in moderate numbers at daylight from 475 to 100 m depth. At night this concentration was restricted to 100-50 m depth; minimum numbers appeared at depths of 600 to 225 m.

Line 90. Two Stations were occupied at daylight, but only Station 90.60 was completely sampled. At Station 90.90, samples corresponded to 25 m intervals from 75 to 0 m. At night, three Stations were occupied but samples were missed at 350-100 m at Station 90.90. No *S. scrippsae* appeared in the upper three daylight hauls (at 75-0 m strata). At night the species was absent from the upper three hauls at the Station closest to shore, and from the upper two hauls (50-0 m strata) at the other two Stations. The species was not observed at 600-350 m at Station 90.45, nor at 225-100 m at Station 90.60. During daylight, moderate numbers were found at 350-225 m, decreasing below and above these depths to 600 m and 75 m, respectively. At night, a moderate concentration occurred at 225-100 m at the Station closest

TABLE B

DAY AND NIGHT AVERAGE AND TOTAL AVERAGE OF *S. SCRIPPSAE* POPULATION PER CRUISE, STATION AND DEPTH

Cruise	Stat.70.60		Stat. 70.75		Stat. 70.90		Stat. 70.110		Average		TOTAL AVERAGE
Depth,m	day	night	day	night	day	night	day	night	day	night	
6902-03											
15-0	-	-	28	1	-	-	-	-	28	1	14
25-0/15	0	0	0	1	-	-	-	-	0	0.5	0.25
50-25	-	0	61	6	-	-	-	-	61	3	22
75-50	0	-	613	-	-	-	-	-	306	-	306
100-75	98	-	8	-	-	-	-	-	53	-	53
125-100	27	-	29	-	-	-	-	-	28	-	28
150-125	27	-	29	-	-	-	-	-	28	-	28
175-150	92	-	29	-	-	-	-	-	60	-	60
200-175	92	-	29	-	-	-	-	-	60	-	60
225-200	0	-	29	-	-	-	-	-	14	-	14
250-225	0	-	347	-	-	-	-	-	173	-	173
275-250	-	-	347	-	-	-	-	-	347	-	347
300-275	-	-	347	-	-	-	-	-	347	-	347
325-300	-	-	347	-	-	-	-	-	347	-	347
350-325	-	-	347	-	-	-	-	-	347	-	347
	Stat, 90.45		Stat.90.60		Stat. 90.90						
15-0	0	0	0	0	-	-			0	0	0
25-15	0	0	0	0	-	-			0	0	0
40-25	0	0	1	0	-	-			0.5	0	0.25
50-40	0	0	0	0	-	-			0	0	0
60/75-50	0	0	0	0	-	-			0	0	0
95/100-75	3	6	31	2	-	-			17	4	1.05
125-100	28	6	126	110	-	-			77	58	67
150-125	2	12	126	110	-	-			64	61	62
175-150	1	12	126	110	-	-			63	61	62
200-175	25	-	188	-	-	-			106	-	106
225-200	18	-	97	-	-	-			57	-	57
250-225	18	-	-	-	-	-			18	-	18
	Stat. 120.45		Stat. 120.55		Stat. 120.70		Stat. 120.90				
15-0	0	0	0	0	0	0	0	0	0	0	0
25-15	0	0	-	0	0	0	0	0	0	0	0
50-25	0	0	-	0	0	0	0	0	0	0	0
75-50	0	0	-	0	0	0	-	0	0	0	0
100-75	0	0	0	0	0	0	0	0	0	0	0
125-100	0	-	-	0	0	0	0	0	0	0	0
150-125	-	-	-	0	0	0	0	0	0	0	0
175-150	1	-	-	0	-	0	0	-	0.5	0	0.25
200-175	1	-	-	0	-	0	0	-	0.5	0	0.25
225-200	-	-	-	-	-	-	0	-	0	-	0
250-225	-	-	-	-	-	-	0	-	0	-	0
275-250	-	-	-	-	-	-	0	-	0	-	0
300-275	-	-	-	-	-	-	0	-	0	-	0

TABLE B (Continuation)

Cruise	Stat. 70.60		Stat. 70.75		Stat. 70.90		Stat. 70.110		Average		TOTAL AVERAGE
Depth, m	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	
6905-60											
25-0	0	0	0	0	0	0	0	0	0	0	0
50-25	0	17	0	26	0	18	-	0	0	15	3
75-50	146	18	307	45	0	11	-	22	151	24	25
100-75	59	68	233	80	26	88	-	20	106	64	78.4
125-100	38	62	21	25	137	0	57	0	64	22	43
150-125	38	62	21	25	137	0	57	0	64	22	43
175-150	38	62	21	25	137	0	57	0	64	22	43
200-175	38	62	21	25	137	0	57	0	64	22	43
225-200	38	62	21	25	137	0	57	0	64	22	43
250-225	-	124	43	84	49	51	13	10	35	67	53.4
275-250	-	124	43	84	49	51	13	10	35	67	53.4
300-275	-	124	43	84	49	51	13	10	35	67	53.4
325-300	-	124	43	84	49	51	13	10	35	67	53.4
350-325	-	124	43	84	49	51	13	10	35	67	53.4
375-350	6	4	8	11	68	45	11	2	23	15	19.3
400-375	6	4	8	11	68	45	11	2	23	15	19.3
425-400	6	4	8	11	68	45	11	2	23	15	19.3
450-425	6	4	8	11	68	45	11	2	23	15	19.3
475-450	6	4	8	11	68	45	11	2	23	15	19.3
500-475	0	2	0	8	0	0	-	1	0	3	1.5
525-500	0	2	0	8	0	0	-	1	0	3	1.5
550-525	0	2	0	8	0	0	-	1	0	3	1.5
575-550	0	2	0	8	0	0	-	1	0	3	1.5
600-575	0	2	0	8	0	0	-	1	0	3	1.5
	Stat. 90.45		Stat. 90.60		Stat. 90.90						
25-0	-	0	0	0	0	0			0	0	0
50-25	-	0	0	0	0	0			0	0	0
75-50	-	0	0	4	0	2			0	2	1.2
100-75	-	1	13	13	-	2			13	5.6	7
125-100	-	14	20	0	-	-			20	7	11
150-125	-	14	20	0	-	-			20	7	11
175-150	-	14	20	0	-	-			20	7	11
200-175	-	14	20	0	-	-			20	7	11
225-200	-	14	20	0	-	-			20	7	11
250-225	-	9	47	24	-	-			47	16	26
275-250	-	9	47	24	-	-			47	16	26
300-275	-	9	47	24	-	-			47	16	26
325-300	-	9	47	24	-	-			47	16	26
350-325	-	9	47	24	-	-			47	16	26
375-350	-	0	16	2	-	28			16	10	11.5
400-375	-	0	16	2	-	28			16	10	11.5
425-400	-	0	16	2	-	28			16	10	11.5
450-425	-	0	16	2	-	28			16	10	11.5
475-450	-	0	16	2	-	28			16	10	11.5
500-475	-	0	1	2	-	8			1	3	2.7
525-500	-	0	1	2	-	8			1	3	2.7
550-525	-	0	1	2	-	8			1	3	2.7
575-550	-	0	1	2	-	8			1	3	2.7
600-575	-	0	1	2	-	8			1	3	2.7
	Stat. 120.45		Stat. 120-55		Stat. 120.70		Stat. 120.90				
25-0	0	0	0	0	0	0	0	0	0	0	0
50-25	0	0	0	0	0	0	-	0	0	0	0
75-50	0	0	0	17	1	0	0	0	0.2	4	2.2
100-75	0	0	-	0	-	0	-	0	0	0	0
125-100	0	1	0	1	0	0	-	0	0	0.5	0.3
150-125	0	1	0	1	0	0	-	0	0	0.5	0.3
175-150	0	1	0	1	0	0	-	0	0	0.5	0.3
200-175	0	1	0	1	0	0	-	0	0	0.5	0.3
225-200	0	1	0	1	0	0	-	0	0	0.5	0.3
250-225	1	2	0	0	0	0	-	0	0.3	0.5	0.3
275-250	1	2	0	0	0	0	-	0	0.3	0.5	0.3
300-275	1	2	0	0	0	0	-	0	0.3	0.5	0.3
325-300	1	2	0	0	0	0	-	0	0.3	0.5	0.3
350-325	1	2	0	0	0	0	-	0	0.3	0.5	0.3
375-350	3	0	0	0	1	0	0	0	1	0	0.5
400-375	3	0	0	0	1	0	0	0	1	0	0.5
425-400	3	0	0	0	1	0	0	0	1	0	0.5
450-425	3	0	0	0	1	0	0	0	1	0	0.5
475-450	3	0	0	0	1	0	0	0	1	0	0.5
500-475	1	0	0	-	2	0	-	0	1	0	0.6
525-500	1	0	0	-	2	0	-	0	1	0	0.6
550-525	1	0	0	-	2	0	-	0	1	0	0.6
575-550	1	0	0	-	2	0	-	0	1	0	0.6
600-575	1	0	0	-	2	0	-	0	1	0	0.6

TABLE B (Continuation)

Cruise	Stat. 70.60		Stat. 70.75		Stat. 70.90		Stat. 70.110		Average		TOTAL
Depth m	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	AVERAGE
6908-09											
25-0	-	-	-	-	-	-	0	0	0	0	0
50-25	-	-	-	-	540	40	-	-	540	0	58
75-50	-	-	-	895	415	116	0	0	41	306	200
100-75	-	-	-	174	352	52	378	1596	224	593	445
125-100	149	-	252	421	20	-	154	665	114	543	257
150-125	149	-	252	421	20	-	154	665	114	543	257
175-150	149	-	252	421	20	-	154	665	114	543	257
200-175	149	-	252	421	20	-	154	665	114	543	257
225-200	149	-	252	421	20	-	154	665	114	543	257
250-225	180	-	40	81	24	27	101	136	86	81	84
275-250	180	-	40	81	24	27	101	136	86	81	84
300-275	180	-	40	81	24	27	101	136	86	81	84
325-300	180	-	40	81	24	27	101	136	86	81	84
350-325	180	-	40	81	24	27	101	136	86	81	84
375-350	0	-	2	31	0	16	45	33	12	26	18
400-375	0	-	2	31	0	16	45	33	12	26	18
425-400	0	-	2	31	0	16	45	33	12	26	18
450-425	0	-	2	31	0	16	45	33	12	26	18
475-450	0	-	2	31	0	16	45	33	12	26	18
500-475	0	-	-	-	-	-	-	1	0	1	0.5
525-500	0	-	-	-	-	-	-	1	0	1	0.5
550-525	0	-	-	-	-	-	-	1	0	1	0.5
575-550	0	-	-	-	-	-	-	1	0	1	0.5
600-575	0	-	-	-	-	-	-	1	0	1	0.5
	Stat. 90.45		Stat. 90.60		Stat. 90.90						
25-0	0	0	0	0	0	0			0	0	0
50-25	0	0	0	0	0	0			0	0	0
75-50	0	0	2	1	6	12			2.6	4	3.5
100-75	72	0	5	24	0	12			25.6	12	19
125-100	-	43	21	19	8	25			14.5	29	23
150-125	-	43	21	19	8	25			14.5	29	23
175-150	-	43	21	19	8	25			14.5	29	23
200-175	-	43	21	19	8	25			14.5	29	23
225-200	-	43	21	19	8	25			14.5	29	23
250-225	-	-	52	18	-	-			52	18	35
275-250	-	-	52	18	-	-			52	18	35
300-275	-	-	52	18	-	-			[illegible]	18	[illegible]
325-300	-	-	[illegible]	18	-	-			52	18	35
350-325	-	-	[illegible]	18	-	-			52	18	35
375-350	2	1	35	47	5	0			14	16	16
400-375	2	1	35	47	5	0			14	16	16
425-400	2	1	35	47	5	0			14	16	16
450-425	2	1	[illegible]	47	5	0			14	16	16
475-450	2	1	[illegible]	47	5	0			14	16	16
500-475	0	0		[illegible]	0	0			0	4	2
525-500	0	0	[illegible]	12	0	0			0	4	2
550-525	0	0		1	0	0			0	4	2
575-550	0	[illegible]		1	0	0			0	4	2
600-575	[illegible]	[illegible]		1	0	[illegible]			0	4	2
	Stat. 120.45		Stat. [illegible]		Stat. [illegible]		Stat. 120.90				
25-0	0	0	0	0	0	0	0	0	0	0	0
50-25	0			0	0	0	0	0	0	0	0
75-50	0	0		-	[illegible]	0	0	0	0	0	0
100-75	0	[illegible]	[illegible]		0	[illegible]	0	0	1.2	0.5	0.9
125-100	1	0	10	[illegible]	1	0	0	0	[illegible]	3	3
150-125	1		10	[illegible]	1	0	0	0	[illegible]	3	3
175-150	1		10	1	1	[illegible]	0	0	[illegible]	[illegible]	3
200-175	1	[illegible]	[illegible]	1	1	[illegible]	0	0	3	[illegible]	3
225-200	1	[illegible]	[illegible]	[illegible]	1	[illegible]	0	0	[illegible]	3	3
250-225	0	1	1	[illegible]	0	[illegible]	1	0	0.5	[illegible]	2
275-250	0	1	1	[illegible]	0	0	1	0	0.5	4	2
300-275	0	1	1	14	[illegible]	0	1	0	0.5	4	2
325-300	0	1	1	[illegible]		[illegible]	1	0	0.5	4	2
350-325	0	1	1	[illegible]	[illegible]		1	0	0.5	4	2
375-350	0	1	1	1	0		1	1	0.5	0.7	0.6
400-375	0	1	1	1	0	[illegible]	1	1	0.5	0.7	0.6
425-400	0	1	[illegible]	1	0		1	1	0.5	0.7	0.6
450-425	0	1	[illegible]	1	[illegible]		1	1	0.5	0.7	0.6
475-450		[illegible]	1	1		[illegible]	1	1	0.5	0.7	0.6
500-475	[illegible]		[illegible]	[illegible]		[illegible]	0	0	0	0	0
525-500	[illegible]	[illegible]		[illegible]		[illegible]	0	0	0		0
550-525			[illegible]	[illegible]			0	0	0	[illegible]	0
575-550	[illegible]		[illegible]	[illegible]	[illegible]		0	0	0		0
600-575		[illegible]		[illegible]			0	0	0	[illegible]	0

TABLE B (Continuation)

Cruise Depth m	Stat. 70.60		Stat. 70.75		Stat. 70.90		Stat. 70.110		Average		TOTAL AVERAGE
	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	
6911-12											
25-0	0	0	0	-	-	-	-	-	0	0	0
50-25	0	0	0	-	-	-	-	-	0	0	0
75-50	0	0	16	-	-	-	-	-	8	0	5
100-75	0	8	172	-	-	-	-	-	86	8	60
125-100	-	448	44	-	-	-	-	-	44	448	246
150-125	-	448	44	-	-	-	-	-	44	448	246
175-150	-	448	44	-	-	-	-	-	44	448	246
200-175	-	448	44	-	-	-	-	-	44	448	246
225-200	-	448	44	-	-	-	-	-	44	448	246
250-225	14	21	25	-	-	-	-	-	18	21	20
275-250	14	21	25	-	-	-	-	-	18	21	20
300-275	14	21	25	-	-	-	-	-	18	21	20
325-300	14	21	25	-	-	-	-	-	18	21	20
350-325	14	21	25	-	-	-	-	-	18	21	20
375-350	56	31	86	-	-	-	-	-	71	31	57
400-375	56	31	86	-	-	-	-	-	71	31	57
425-400	56	31	86	-	-	-	-	-	71	31	57
450-425	56	31	86	-	-	-	-	-	71	31	57
475-450	56	31	86	-	-	-	-	-	71	31	57
500-475	506	370	1	-	-	-	-	-	253	370	292
525-500	506	370	1	-	-	-	-	-	253	370	292
550-525	506	370	1	-	-	-	-	-	253	370	292
575-550	506	370	1	-	-	-	-	-	253	370	292
600-575	506	370	1	-	-	-	-	-	253	370	292
	Stat.	90.45	Stat.	90.60	Stat.	90.90					
25-0	-	0	0	0	0	0			0	0	0
50-25	0	-	0	0	0	-			0	0	0
75-50	2	0	0	0	0	-			0.7	0	0.4
100-75	1	4	0	-	0	-			0.3	4	1
125-100	-	0	48	-	4	4			21	2	14
150-125	-	0	48	-	4	4			21	2	14
175-150	-	0	48	-	4	4			21	2	14
200-175	-	0	48	-	4	4			21	2	14
225-200	-	0	48	-	4	4			21	2	14
250-225	-	0	24	34	-	-			24	17	19
275-250	-	0	24	34	-	-			24	17	19
300-275	-	0	24	34	-	-			24	17	19
325-300	-	0	24	34	-	-			24	17	19
350-325	-	0	24	34	-	-			24	17	19
375-350	-	-	38	5	30	-			34	5	24
400-375	-	-	38	5	30	-			34	5	24
425-400	-	-	38	5	30	-			34	5	24
450-425	-	-	38	5	30	-			34	5	24
475-450	-	-	38	5	30	-			34	5	24
500-475	-	-	-	31	-	-			-	31	31
525-500	-	-	-	31	-	-			-	31	31
550-525	-	-	-	31	-	-			-	31	31
575-550	-	-	-	31	-	-			-	31	31
600-575	-	-	-	31	-	-			-	31	31
	Stat.	120.45	Stat.	120.55	Stat.	120.70	Stat.	120.90			
5-0	0	0	0	0	0	0	0	0	0	0	0
50-25	0	0	0	0	0	0	0	0	0	0	0
75-50	0	0	0	0	0	0	0	0	0	0	0
100-75	0	0	-	0	0	0	0	0	0	0	0
125-100	0	0	0	0	0	0	0	0	0	0	0
150-125	0	0	0	0	0	0	0	0	0	0	0
175-150	0	0	0	0	0	0	0	0	0	0	0
200-175	0	0	0	0	0	0	0	0	0	0	0
225-200	0	0	0	0	0	0	0	0	0	0	0
250-225	0	0	0	0	0	0	-	0	0	0	0
275-250	0	0	0	0	0	0	-	0	0	0	0
300-275	0	0	0	0	0	0	-	0	0	0	0
325-300	0	0	0	0	0	0	-	0	0	0	0
350-325	0	0	0	0	0	0	-	0	0	0	0
375-350	0	0	0	0	0	0	0	0	0	0	0
400-375	0	0	0	0	0	0	0	0	0	0	0
425-400	0	0	0	0	0	0	0	0	0	0	0
450-425	0	0	0	0	0	0	0	0	0	0	0
475-450	0	0	0	0	0	0	0	0	0	0	0
500-475	0	0	0	0	0	0	0	0	0	0	0
525-500	0	0	0	0	0	0	0	0	0	0	0
550-525	0	0	0	0	0	0	0	0	0	0	0
575-550	0	0	0	0	0	0	0	0	0	0	0
600-575	0	0	0	0	0	0	0	0	0	0	0

TABLE C

AVERAGE TOTAL NUMBER OF *SAGITTA SCRIPPSAE* AT EACH 25 m DEPTH INTERVAL, FROM 0 TO 600 m

Station Depth, m	70.60	70.75	70.90	70.110	Average per Stat. Line 70	90.45	90.60	90.90	Average per Stat Line 90	120.45	120.55	120.70	120.90	Average per Stat. Line 120
25-0	0	6	0	0	2	0	0	0	0	0	0	0	0	0
50-25	3	19	150	0	43	0	<1	0	1	0	0	0	0	0
75-50	33	375	135	7	138	1	1	4	2	0	3	0.1	0	0.8
100-75	40	133	130	665	242	12	8	4	8	0	1	0.3	0	0.3
125-100	150	132	52	219	138	15	44	12	24	0.4	3.2	0.2	0	1.0
150-125	150	132	52	219	138	15	44	12	24	0.4	3.2	0.2	0	1.0
175-150	150	132	52	219	138	15	44	12	24	0.4	3.2	0.2	0	1.0
200-175	150	132	52	219	138	15	44	12	24	0.4	3.2	0.2	0	1.0
225-200	150	132	52	219	138	15	44	12	24	0.4	3.2	0.2	0	1.0
250-225	85	103	33	65	73	4	33	14	17	0.6	2.4	0	0.2	0.8
275-250	85	103	33	65	73	4	33	14	17	0.6	2.4	0	0.2	0.8
300-275	85	103	33	65	73	4	33	14	17	0.6	2.4	0	0.2	0.8
325-300	85	103	38	65	73	4	33	14	17	0.6	2.4	0	0.2	0.8
350-325	85	103	38	65	73	4	33	14	17	0.6	2.4	0	0.2	0.8
375-350	19	28	32	23	26	1	24	16	13	0.6	0.4	0.2	0.4	0.4
400-375	19	28	32	23	26	1	24	16	13	0.6	0.4	0.2	0.4	0.4
425-400	19	28	32	23	26	1	24	16	13	0.6	0.4	0.2	0.4	0.4
450-425	19	28	32	23	26	1	24	16	13	0.6	0.4	0.2	0.4	0.4
75-450	19	28	32	23	26	1	24	16	13	0.6	0.4	0.2	0.4	0.4
500-475	176	3	0	1	45	0	9	3	4	0.2	0	0.4	0	0.2
525-500	176	3	0	1	45	0	9	3	4	0.2	0	0.4	0	0.2
550-525	.176	3	0	1	45	0	9	3	4	0.2	0	0.4	0	0.2
575-550	176	3	0	1	45	0	9	3	4	0.2	0	0.4	0	0.2
00-575	176	3	0	1	45	0	9	3	4	0.2	0	0.4	0	0.2
Total :	2227	1863	1027	2211	1833	112	559	231	301	9	34	4.4	3.4	13.1
Above 150 m:	376	797	519	1110	701	43	98	32	59	0.8	10.4	0.8	0	3.1
% of total :	16.9	42.8	50.5	50.2	38.2	38.4	17.5	13.9	19.6	8.9	30.6	18.2	0	23,7

TABLE D

TOTAL AND AVERAGE NUMBER OF *S. SCRIPPSAE* PER DAY, NIGHT, LINE OF STATIONS, AND SEASON

Cruise Line of Stations	Line 70 Day	Line 70 Night	Line 90 Day	Line 90 Night	Line 120 Day	Line 120 Night	Total Day	Total Night	TOTAL
6902-03									
Number specimens	2930	8	790	368	2	0	3703	376	4070
Average number	225	1.6	43	24	0.08	0	67	8	39.9
6905-06									
Number specimens	3026	2558	433	457	41	37	3500	3052	6552
Average number	111	79	39	20	16	1.2	56	36	43.6
6908-09									
Number specimens	6520	9923	700	874	85	152	7305	10949	18254
Average number	343	620	37	39	3.5	6.6	101	158	146
6911-12									
Number specimens	3848	4350	723	374	0	0	4571	4724	9295
Average number	256	570	90	28	0	0	58	88	103

to shore, and progressed offshore at two separate levels: 100-75 m and 350-225 m. At the Station farthest offshore, moderate numbers, occurred only at 475-350 m depth, with low concentrations at 100-50 m and below 475 m depth. At Station 90.45, the lowest number occurred at 100-75 m and 350-225 m depth.

Line 120. All Stations on this Line were covered, both during daylight and at night. Daylight hauls, however, were missing at 100-75 m for Stations 120.55 and 120.70; and at 50-25 m, 350-75 m, and 600-475 m for Station 120.90. Night hauls at 600-475 m for Station 120.55 were also missing. *S. crippsae* was present in 6 of the 25 daylight hauls made, and in 4 of 31 night hauls. During daylight, the species appeared in low concentrations at 600-225 m depth at Station 120.45, and at 75-50 m and 600-350 m at Station 120.70. It was found in low concentration at 350-100 m at Station 120.45 during the night. At Station 120.55, it occurred in moderate concentration at 75-50 m, and low concentration at 225-100 m. This southerly extension of the *S. scrippsae* population appears relatively close to shore.

AUGUST-SEPTEMBER 1969 CRUISE (6908-09). Figure 3.

Line 70. During this cruise, all four Stations were occupied on this Line during daylight. At night, only three Stations were covered (no hauls were taken at Station 70.60). However, daylight hauls were missing for depths of 100 to 0 m from Station 70.60 and 70.75; at 600-475 m from Stations 70.75, 70.90, and 70.110; and at 25-0 m and 50-25 m from Stations 70.90 and 70.110, respectively Night hauls were missing from depths of 50-0 m, 25-0 m, and 50-25 m from Stations 70.75, 70.90, and 70.110, respectively; at 600-475 m from Stations 70.75 and 70.90; and at 225-100 m for Station 70.90.

A high concentration of *S. scrippsae* occurred at 350-100 m depth of Station 70.60 during daylight. At Station 70.75, a high concentration

TABLE F

DAY AND NIGHT STRUCTURE OF THE POPULATION OF S. *SCRIPPSAE* (NUMBERS PER SIZE
STATION AND DEPTH)

Cruises 6902-03	Depth (m)	Day							Night						
		Size (mm)							Size (mm)						
		<10	10-20	21-30	31-40	41-50	51-60	Total	<10	10-20	21-30	31-40	41-50	51-60	Total
Station															
70.60	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	-	-	-	-	-	-	-	0	0	0	0	0	0	0
	75-50	0	0	0	0	0	0	0	-	-	-	-	-	-	-
	112-75	0	46	49	3	0	0	98	-	-	-	-	-	-	-
	160-112	0	6	38	10	0	0	54	-	-	-	-	-	-	-
	208-160	0	12	148	24	0	0	184	-	-	-	-	-	-	-
	256-208	0	0	0	0	0	0	0	-	-	-	-	-	-	-
70.75	15-0	0	8	20	0	0	0	28	-	-	1	0	0	0	1
	25-15	0	0	0	0	0	0	0	0	0	0	1	0	0	1
	50-25	0	57	4	0	0	0	61	0	2	4	0	0	0	6
	75-50	0	367	231	15	0	0	613	-	-	-	-	-	-	-
	100-75	0	0	4	4	0	0	8	-	-	-	-	-	-	-
	225-100	0	10	80	55	0	0	145	-	-	-	-	-	-	-
	350-225	0	0	740	975	20	0	1735	-	-	-	-	-	-	-
70.90	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
70.110	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
90.45	15-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	25-15	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	40-25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-40	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	60-50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	95-60	0	3	0	0	0	0	3	0	6	0	0	0	0	6
	130-95	0	26	2	0	0	0	28	0	0	3	3	0	0	6
	168-130	0	0	3	0	0	0	3	0	1	22	1	0	0	24
	203-168	0	0	23	2	0	0	25	-	-	-	-	-	-	-
	240-203	0	0	30	6	0	0	36	-	-	-	-	-	-	-
90.60	11-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	22-11	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	34-22	0	0	1	0	0	0	1	0	0	0	0	0	0	0
	50-34	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	75-50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	100-75	0	0	0	31	0	0	31	0	0	2	0	0	0	2
	176-100	0	60	318	0	0	0	378	0	72	255	3	0	0	330
	213-176	0	21	260	4	0	0	285	-	-	-	-	-	-	-
90.90	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
120.45	15-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	25-15	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	75-50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	100-75	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	125-100	0	0	0	0	0	0	0	-	-	-	-	-	-	-
	200-250	0	0	2	0	0	0	2	-	-	-	-	-	-	-
120.55	15-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	25-15	-	-	-	-	-	-	-	0	0	0	0	0	0	0
	50-25	-	-	-	-	-	-	-	0	0	0	0	0	0	0
	75-50	-	-	-	-	-	-	-	0	0	0	0	0	0	0
	100-75	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	125-100	-	-	-	-	-	-	-	0	0	0	0	0	0	0
	150-125	-	-	-	-	-	-	-	0	0	0	0	0	0	0
	200-150	-	-	-	-	-	-	-	0	0	0	0	0	0	0
120.70	15-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	25-15	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	75-50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	100-75	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	125-100	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	150-125	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	200-150	-	-	-	-	-	-	-	0	0	0	0	0	0	0
120.90	15-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	25-15	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	75-50	-	-	-	-	-	-	-	0	0	0	0	0	0	0
	100-75	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	150-100	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	200-150	0	0	0	0	0	0	0	-	-	-	-	-	-	-
	250-200	0	0	0	0	0	0	0	-	-	-	-	-	-	-
	300-250	0	0	0	0	0	0	0	-	-	-	-	-	-	-

TABLE F (Continuation)

Cruises 6905-06	Depth (m)	Day							Night						
		Size (mm)							Size (mm)						
		<10	10-20	21-30	31-40	41-50	51-60	Total	<10	10-20	21-30	31-40	41-50	51-60	Total
Station															
70.60	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	0	12	1	2	2	0	17
	75-50	0	125	21	0	0	0	146	0	2	7	7	2	0	18
	100-75	0	8	46	5	0	0	59	0	21	33	12	2	0	68
	225-100	0	0	.30	150	10	0	190	0	0	35	230	45	0	310
	350-225	-	-	-	-	-	-	-	0	0	135	245	235	5	620
	475-350	0	0	0	10	20	0	30	0	0	10	10	0	0	20
	600-475	0	0	0	0	0	0	0	0	0	0	0	5	0	5
70.75	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	0	0	4	22	0	0	26
	75-50	0	122	127	51	7	0	307	0	2	28	14	1	0	45
	100-75	0	76	152	5	0	0	233	0	11	41	28	0	0	80
	225-100	0	0	45	45	15	0	105	0	0	65	60	0	0	125
	350-225	0	0	20	155	40	0	215	0	0	10	305	105	0	420
	475-350	0	0	30	10	0	0	40	0	0	5	50	0	0	55
	600-475	0	0	0	0	0	0	0	0	0	0	40	0	0	40
70.70	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	1	16	0	1	0	0	18
	75-50	0	0	0	0	0	0	0	0	0	0	11	0	0	11
	100-75	0	20	6	0	0	0	26	0	11	60	17	0	0	88
	225-100	0	45	335	290	15	0	685	0	0	0	0	0	0	0
	350-225	0	0	75	170	0	0	245	0	0	105	150	0	0	255
	475-350	0	0	30	285	25	0	340	0	0	25	190	10	0	225
	600-475	0	0	0	0	0	0	0	0	0	0	0	0	0	0
70.110	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	-	-	-	-	-	-	-	0	0	0	0	0	0	0
	75-50	-	-	-	-	-	-	-	1	21	0	0	0	0	22
	100-75	-	-	-	-	-	-	-	0	20	0	0	0	0	20
	275-100	0	230	55	0	0	0	285	0	0	0	0	0	0	0
	350-225	0	0	65	0	0	0	65	0	10	40	0	0	0	50
	475-350	0	5	50	0	0	0	55	0	0	10	0	0	0	10
	600-475	-	-	-	-	-	-	-	0	0	5	0	0	0	5
90.45	25-0	-	-	-	-	-	-	-	0	0	0	0	0	0	0
	50-25	-	-	-	-	-	-	-	0	0	0	0	0	0	0
	75-50	-	-	-	-	-	-	-	0	0	0	0	0	0	0
	100-75	-	-	-	-	-	-	-	0	0	0	1	0	0	1
	225-100	-	-	-	-	-	-	-	0	5	25	35	5	0	70
	350-225	-	-	-	-	-	-	-	0	0	20	20	5	0	45
	475-350	-	-	-	-	-	-	-	0	0	0	0	0	0	0
	600-475	-	-	-	-	-	-	-	0	0	0	0	0	0	0
90.60	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	75-50	0	0	0	0	0	0	0	0	0	4	0	0	0	4
	100-75	0	6	6	1	0	0	13	0	0	9	4	0	0	13
	225-100	0	35	65	0	0	0	100	0	0	0	0	0	0	0
	350-225	0	20	185	30	0	0	235	0	0	75	45	0	0	120
	475-350	0	20	60	0	0	0	80	0	0	5	5	0	0	10
	600-475	0	0	5	0	0	0	5	0	0	0	10	0	0	10
90.90	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	75-70	0	0	0	0	0	0	0	0	0	1	1	0	0	2
	100-75	-	-	-	-	-	-	-	0	2	0	0	0	0	2
	225-100	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	350-225	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	475-350	-	-	-	-	-	-	-	0	0	120	20	0	0-	140
	600-475	-	-	-	-	-	-	-	0	0	15	20	5	0	40
120.45	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	75-50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	100-75	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	225-100	0	0	0	0	0	0	0	0	5	0	0	0	0	5
	350-225	0	5	0	0	0	0	5	0	0	10	0	0	0	10
	475-350	0	5	10	0	0	0	15	0	0	0	0	0	0	0
	600-475	0	0	5	0	0	0	5	0	0	0	0	0	0	0
120.55	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	75-50	0	0	0	0	0	0	0	0	13	4	0	0	0	17
	100-75	-	-	-	-	-	-	-	0	0	0	0	0	0	0
	225-100	0	0	0	0	0	0	0	0	5	0	0	0	0	5
	350-225	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	475-350	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	600-475	0	0	0	0	0	0	0	-	-	-	-	-	-	-
120.70	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	75-50	0	1	0	0	0	0	1	0	0	0	0	0	0	0
	100-75	-	-	-	-	-	-	-	0	0	0	0	0	0	0
	225-100	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	350-225	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	475-350	0	0	5	0	0	0	5	0	0	0	0	0	0	0
	600-475	0	0	0	10	0	0	10	0	0	0	0	0	0	0
120.90	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	-	-	-	-	-	-	-	0	0	0	0	0	0	0
	75-50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	100-75	-	-	-	-	-	-	-	0	0	0	0	0	0	0
	225-100	-	-	-	-	-	-	-	0	0	0	0	0	0	0
	350-225	-	-	-	-	-	-	-	0	0	0	0	0	0	0
	475-350	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	600-475	-	-	-	-	-	-	-	0	0	0	0	0	0	0

TABLE E (Continuation)

Cruises 6911-12	Depth (m)	Day							Night						
		Sizes (mm)							Sizes (mm)						
		<10	10-20	21-30	31-40	41-50	51-60	Total	< 10	10-20	21-30	31-40	41-50	51-60	Total
Station															
70.60	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	75-50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	100-75	0	0	0	0	0	0	0	0	0	2	6	0	0	8
	225-100	-	-	-	-	-	-	-	0	135	1545	560	10	0	2240
	350-225	0	0	40	30	0	0	70	0	0	85	20	0	0	105
	475-350	0	0	70	210	0	0	280	0	0	35	120	0	0	155
	600-475	0	290	1460	780	0	0	2530	0	470	1020	360	0	0	1850
70.75	25-0	0	0	0	0	0	0	0	-	-	-	-	-	-	-
	50-25	0	0	0	0	0	0	0	-	-	-	-	-	-	-
	75-50	0	12	4	0	0	0	16	-	-	-	-	-	-	-
	100-75	0	46	121	5	0	0	172	-	-	-	-	-	-	-
	225-100	0	5	175	40	0	0	220	-	-	-	-	-	-	-
	350-225	0	0	40	85	0	0	125	-	-	-	-	-	-	-
	475-350	0	0	195	235	0	0	430	-	-	-	-	-	-	-
	600-475	0	0	5	0	0	0	5	-	-	-	-	-	-	-
70.90	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
70.110	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
90.45	25-0	-	-	-	-	-	-	-	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	-	-	-	-	-	-	-
	75-50	0	2	0	0	0	0	2	0	0	0	0	0	0	0
	100-75	0	0	1	0	0	0	1	0	4	0	0	0	0	4
	225-100	-	-	-	-	-	-	-	0	0	0	0	0	0	0
	350-225	-	-	-	-	-	-	-	0	0	0	0	0	0	0
	475-350	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	600-475	-	-	-	-	-	-	-	-	-	-	-	-	-	-
90.60	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	75-50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	100-75	0	0	0	0	0	0	0	-	-	-	-	-	-	-
	225-100	0	150	90	0	0	0	240	-	-	-	-	-	-	-
	350-225	0	20	85	15	0	0	120	0	35	125	10	0	0	170
	475-350	0	35	135	20	0	0	190	0	0	25	0	0	0	25
	600-475	-	-	-	-	-	-	-	0	10	130	15	0	0	155
90.90	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	-	-	-	-	-	-	-
	75-50	0	0	0	0	0	0	0	-	-	-	-	-	-	-
	100-75	0	0	0	0	0	0	0	-	-	-	-	-	-	-
	225-100	0	5	15	0	0	0	20	0	5	15	0	0	0	20
	350-225	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	475-350	0	5	125	20	0	0	150	-	-	-	-	-	-	-
	600-475	-	-	-	-	-	-	-	-	-	-	-	-	-	-
120.45	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	75-50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	100-75	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	225-100	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	350-225	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	475-350	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	600-475	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120.55	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	75-50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	100-75	-	-	-	-	-	-	-	0	0	0	0	0	0	0
	225-100	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	350-225	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	475-350	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	600-475	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120.70	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	75-50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	100-75	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	225-100	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	350-225	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	475-350	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	600-475	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120.90	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	75-50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	100-75	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	225-100	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	350-225	-	-	-	-	-	-	-	0	0	0	0	0	0	0
	475-350	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	600-475	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE E. (Continuation)

Cruises 6908-09	Depth (m)	Day							Night						
		Sizes (mm)							Sizes (mm)						
		<10	10-20	21-30	31-40	41-50	51-60	Total	<10	10-20	21-30	31-40	41-50	51-60	Total
Station															
70.60	25-0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	50-25	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	75-50	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	100-75	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	225-100	0	100	555	80	10	0	745	-	-	-	-	-	-	-
	350-225	0	50	700	140	10	0	900	-	-	-	-	-	-	-
	475-350	0	0	0	0	0	0	0	-	-	-	-	-	-	-
	600-475	0	0	0	0	0	0	0	-	-	-	-	-	-	-
70.75	25-0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	50-25	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	75-50	-	-	-	-	-	-	-	0	161	456	271	7	0	895
	100-75	-	-	-	-	-	-	-	0	0	92	80	2	0	174
	225-100	-	20	620	580	40	-	1260	0	35	1265	785	20	0	2105
	350-225	0	5	70	115	10	-	200	0	0	80	310	15	0	405
	475-350	0	0	0	10	0	0	10	0	0	30	120	5	0	155
	600-475	-	-	-	-	-	-	-	-	-	-	-	-	-	-
70.90	25-0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	50-25	68	440	32	0	0	0	540	0	14	19	6	1	0	40
	75-50	0	110	212	90	3	0	415	0	53	51	10	2	0	116
	100-75	0	160	164	28	0	0	352	2	30	16	4	0	0	52
	275-100	0	15	75	10	0	0	100	-	-	-	-	-	-	-
	350-275	0	0	45	70	5	0	120	0	5	50	75	5	0	135
	475-350	0	0	0	0	0	0	0	0	0	40	35	5	0	80
	600-475	-	-	-	-	-	-	-	-	-	-	-	-	-	-
70.110	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	75-50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	100-75	96	282	0	0	0	0	378	264	1288	44	0	0	0	1596
	225-100	5	725	40	0	0	0	770	260	2240	820	5	0	0	3325
	350-225	0	325	180	0	0	0	505	0	285	320	75	0	0	680
	475-350	0	5	150	70	0	0	225	0	0	105	55	0	0	165
	600-475	-	-	-	-	-	-	-	0	5	0	0	0	0	5
90.45	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	75-50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	100-75	0	70	2	0	0	0	72	0	0	0	0	0	0	0
	225-100	-	-	-	-	-	-	-	-	90	120	5	0	0	215
	350-225	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	475-350	0	0	5	5	0	0	10	0	0	5	0	0	0	5
	600-475	0	0	0	0	0	0	0	0	0	0	0	0	0	0
90.60	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	75-50	0	6	0	0	0	0	6	0	10	2	0	0	0	12
	100-75	0	0	0	0	0	0	0	0	9	8	0	0	0	12
	275-100	0	25	15	0	0	0	40	0	100	25	0	0	0	125
	350-275	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	475-350	0	5	10	10	0	0	25	0	0	0	0	0	0	0
	600-475	0	0	0	0	0	0	0	0	0	0	0	0	0	0
90.90	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	75-50	0	6	0	0	0	0	6	0	10	2	0	0	0	12
	100-75	0	0	0	0	0	0	0	0	4	8	0	0	0	12
	225-100	0	25	15	0	0	0	40	0	100	25	0	0	0	125
	350-225	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	475-350	0	5	10	10	0	0	25	0	0	0	0	0	0	0
	600-475	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120.45	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	75-50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	100-75	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	275-100	0	5	0	0	0	0	5	0	0	0	0	0	0	0
	350-275	0	0	0	0	0	0	0	0	0	5	0	0	0	5
	475-350	0	0	0	0	0	0	0	0	0	5	0	0	0	5
	600-475	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120.55	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	75-50	0	0	0	0	0	0	0	-	-	-	-	-	-	-
	100-75	0	1	4	0	0	0	5	0	0	0	0	0	0	0
	225-100	0	40	10	0	0	0	50	5	45	10	0	0	0	60
	350-225	0	5	0	0	0	0	5	0	55	15	0	0	0	70
	475-350	0	0	5	0	0	0	5	0	0	5	0	0	0	5
	600-475	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120.70	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	75-50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	100-75	0	0	0	0	0	0	0	0	0	0	0	0	0	2
	225-100	0	0	5	0	0	0	5	0	0	0	0	0	0	0
	350-225	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	475-350	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	600-475	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120.90	25-0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50-25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	75-50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	100-75	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	225-100	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	350-225	0	0	5	0	0	0	5	0	0	0	0	0	0	0
	475-350	0	5	0	0	0	0	5	0	0	5	0	0	0	5
	600-475	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE F

AVERAGE DATA ON STRUCTURE OF *S. SCRIPPSAE* POPULATION DURING DAY AND NIGHT AT EACH LINE OF STATIONS DURING THE FOUR SEASONS OF 1969

Cruise Stat. Line	size mm	DAY total	DAY Average	NIGHT Total	NIGHT Average	DAY/NIGHT Total	DAY/NIGHT Average
6902-30							
70.	< 10	0	0	0	0	0	0
	10-20	506	39	2	0.4	508	28
	21-30	1514	101	5	1	1319	73
	31-40	1086	83	2	0.4	1088	60
	41-50	20	1.3	0	0	20	1
	51-60	0	0	0	0	0	0
90.	< 10	0	0	0	0	0	0
	10-20	112	6.2	79	5.3	191	5.7
	21-30	637	35.3	282	18.8	919	27
	31-40	42	2.3	7	0.2	49	1.5
	41-50	0	0	0	0	0	0
	51-60	0	0	0	0	0	0
120.	< 10	0	0	0	0	0	0
	10-20	0	0	0	0	0	0
	21-30	2	0.08	0	0	2	0.03
	31-40	0	0	0	0	0	0
	41-50	0	0	0	0	0	0
	51-60	0	0	0	0	0	0
6905-06							
70.	< 10	0	0	2	0.6	2	0.03
	10-20	631	23.4	126	3.9	757	12.8
	21-30	1087	40.2	619	19	1706	28.9
	31-40	1176	43.5	1394	43.5	2570	43.5
	41-50	132	4.9	407	12.7	539	9
	51-60	0	0	5	0.15	5	0.08
90.	< 10	0	0	0	0	0	0
	10-20	81	7.3	7	0.3	88	2.6
	21-30	321	29.9	274	12.4	595	18
	31-40	31	2.8	161	7.7	192	5.8
	41-50	0	0	15	0.6	15	0.4
	51-60	0	0	0	0	0	0
120.	< 10	0	0	0	0	0	0
	10-20	11	0.45	23	0.7	34	0.6
	21-30	20	0.8	14	0.4	34	0.6
	31-40	10	0.4	0	0	10	0.1
	41-50	0	0	0	0	0	0
	51-60	0	0	0	0	0	0
6908-09							
70.	< 10	169	9.4	526	30.9	695	19.8
	10-20	2237	124.2	4116	242	6553	181.5
	21-30	2843	157.9	3388	199.2	6231	178
	31-40	1193	66.2	1831	107.7	3024	86.4
	41-50	78	4.3	62	3.6	140	8
	51-60	0	0	0	0	0	0
90.	< 10	0	0	0	0	0	0
	10-20	230	10.9	382	17.5	612	14.2
	21-30	415	19.7	457	20.7	872	20.2
	31-40	55	2.6	35	1.5	90	2
	41-50	0	0	0	0	0	0
	51-60	0	0	0	0	0	0
120.	< 10	0	0	5	0.1	5	0.07
	10-20	56	1.7	102	3	158	2.4
	21-30	29	0.9	45	1.4	74	1.15
	31-40	0	0	0	0	0	0
	41-50	0	0	0	0	0	0
	51-60	0	0	0	0	0	0
6911-12							
70.	< 10	0	0	0	0	0	0
	10-20	353	23.5	605	75.6	958	41.6
	21-30	2110	140.6	1142	142.7	3252	141
	31-40	1385	92.3	1066	133.2	4251	106.5
	41-50	0	0	10	1.2	10	0.4
	51-60	0	0	0	0	0	0
90.	< 10	0	0	0	0	0	0
	10-20	217	13.5	54	4	271	9.3
	21-30	451	28	295	22.6	746	25.7
	31-40	55	3.4	25	1.9	80	2.7
	41-50	0	0	0	0	0	0
	51-60	0	0	0	0	0	0
120.	< 10	0	0	0	0	0	0
	10-20	0	0	0	0	0	0
	21-30	0	0	0	0	0	0
	31-40	0	0	0	0	0	0
	41-50	0	0	0	0	0	0
	51-60	0	0	0	0	0	0

TABLE G

TOTAL AND AVERAGE STRUCTURE OF THE POPULATION OF *S. SCRIPPSAE*, DAY/NIGHT COMBINED, FOR THE REGION SURVEYED DURING THE FOUR SEASONS OF 1969

Cruise	size mm	total	Average
6902-03	< 10	0	0
	10-20	699	6.8
	21-30	2240	21.9
	31-40	1137	11.1
	41-50	20	0.19
	51-60	0	0
6905-06	< 10	2	0.01
	10-20	879	5.9
	21-30	2335	15.7
	31-40	2772	18.7
	41-50	554	3.7
	51-60	5	0.03
6908-09	< 10	700	4.9
	10-20	7123	50
	21-30	7177	50.5
	31-40	90	0.6
	41-50	0	0
	51-60	0	0
6911-12	< 10	0	0
	10-20	1229	10.7
	21-30	3998	35
	31-40	2531	22.2
	41-50	10	0.08
	51-60	0	0

appeared during daylight at 225-100 m, with moderate numbers at 350-225 m; minimum numbers occurred at 475-350 m. At night, the highest concentration remained at 225-50 m, with moderate numbers at 475-225 m. The highest concentration at Station 70.90 appeared in daylight at 100-25 m layers, with moderate numbers at 350-100 m. The high concentration at night occurred at 100-75 m, with moderate numbers above and below that layer. At Station 70.110, *S. scrippsae* was abundant at 350-75 m, with moderate numbers at 475-350 m during daylight. At night, the highest concentration observed for the whole year appeared at the

100-75 m depth. Below the 100 m layer, large numbers occurred at 350-100 m, with moderate abundance at 475-350 m. Few specimens were found at a depth of 600-475 m. The high and moderate concentration distribution pattern outlined a waved profile.

Line 90. The three Stations on this Line were all occupied at daylight and night, although samples at various layers were missing for Stations 90.45 and 90.90. *S. scrippsae* was absent from the three layers (75-0 m), two layers (50-0 m), and the 600-475 m depth in daylight, and the four and two upper layers at night. It was also missing at 600-475 m and 600-350 m at Stations closest to, and farthest from, the shore, respectively. At Station 90.45, this species appeared in daylight hauls in moderate concentrations at 100-75 m, with minimum numbers at 475-350 m. At night, moderate concentrations were found at 225-100 m, and minimum numbers at 475-350 m depth. At Station 90.60, *S. scrippsae* was obtained in daylight in moderate concentration extending from 475-100 m, with a minimum at 100-50 m. At night, moderate concentrations were found in the layers from 600 to 75 m, with the lowest amounts at 75-50 m depth. The species appeared in low numbers in daylight at Station 90.90, while moderate numbers occurred at 225-50 m depth during the night.

Line 120. All four Station on this Line were occupied both day and night at the eight stratified intervals per Station, except for level 75-50 m at Station 120.55 at night. *S. scrippsae* was absent from most of the upper and deep layers. At Station 120.45, it was present at 225-100 m and 475-225 m in small numbers in daylight and night, respectively. At Station 120.55, it occurred from 475 to 75 m in minimum concentrations during daylight; at night moderate concentrations appeared at 350 to 100 m depth, decreasing in number to the 475 m depth. At Station 120.70, the species occurred only in low numbers at 225-100 m in daylight and 100-75 m at night. It was found at Station 120.90 in minimum numbers at 475-225 m and 475-350 m in daylight and night, respectively.

The large wave mentioned in the distribution pattern of *S. scrippsae* in the profile of Line 70 was also evident at Line 90, and persisted in sharp outline at Line 120.

NOVEMBER-DECEMBER CRUISE (6911-12). Figure 4.

Line 70. Only three Stations were occupied on this Line: two during the day, and one at night. Samples were also missing for 225-100 m layer at Station 70.60 during daylight. *S. scrippsae* was absent during daylight from the upper four and two layers for inshore and offshore locations, respectively, and from the upper three layers at night. At Station 70.60, high concentrations occurred during daylight at 600-475 m, and moderate numbers at 475-225 m; at night, two centers of high concentration appeared at 600-475 m and minimum at 100-75 m depth. A daylight low concentration occurred at Station 70.75 at 100-75 m depth, with moderate amount at 75-50 m and 475-100 m depth; the minimum occurred at 600-475 m depth. No collections were obtained at night from this locality.

Line 90. The three Stations on this Line were occupied both during the day and at night, but several samples were missing: 25-0 m and 600-100 m during daylight and 50-25 and 600-350 m at night for Station 90.45; 600-475 m during daylight and 225-75 m at night for Station 90.70; and 600-475 m and 350-225 m during daylight, and 600-225 m and 100-25 m at night for Station 90.90. At Station 90.45, *S. scrippsae* was present in minimm amounts at 100-50 m during daylight and at 100-75 m at night. It occurred at Station 90.60 in moderate numbers at 475-100 m during daylight. At night, moderate numbers were found at 350-225 m and 600-475 m, with a minimum at 475-350 m. At Station 90.90, *S. scrippsae* occurred in moderate numbers at 475-350 m, with a minimum at 225-100 m during daylight, and a minimum concentration at 225-100 m at night.

Line 120. All four Stations on this Line were occupied both during the day and at night, and at the eight stratified intervals, except for levels 100-75 m and 350-225 m at Stations 150.55 and 120.90 during the day. However, *S. scrippsae* did not occur at any strata on this Line, either during daylight or at night.

The population of *S. scrippsae* appeared at times more abundant in the upper layers or at various depth strata at night, while in other instances this distributional abundance occurred during daylight. The greatest number of specimens (3325) were obtained during a night haul on the August cruise at Station 70.110 (225 to 100 m depth). On the same cruise, 2105 individuals occurred at Station 70.75 at night and 1260 in daylight at the 225-100 m depth. In November, 2539 specimens were collected in daylight Station 70.60 from the 600-475 m depth. On the same November-December cruise, a similar concentration of individuals was observed at night at the 225-100 m depth at Station 70.60. Slightly lower concentrations were noted here in the 600 to 475 m stratum (Figures 2 and 4, and Tables A and B). Unfortunately, daylight collecctions from the 225 to 100 m stratum, which might have proved useful in comparing the night and day distribution of *S. scrippsae*, are missing for Station 70.60 of the November-December cruise.

The greatest total number of *S. scrippsae* specimens was collected in August-September, followed by the number in November-December. The lowest numbers were obtained on the winter cruise. The amount of *S. scrippsae* obtained in August-September was about twice that of November-December, and three times that of spring (May-June); the lowest concentration occurred in winter (February-March), as seen in Table D.

The seasonal day and night bathymetric distributions of *S. scrippsae* are shown in Tables B and D. The greatest numbers of *S. scrippsae* appeared during summer, then fall, with the lowest occurring during winter. It can be seen that day and night average numbers are similar. The highest average numbers were present during daylight in winter and spring, while in summer and fall they were slightly greater at night. Comparing data at same depths for both day and night series, indicates that equal numbers of *S. scrippsae* were taken, on the average, in both series.

In February-March, the number of specimens decreased about 63% from Line 70 to Line 90 in day and night populations combined, and decreased about 100% from these Lines to Line 120. In May-June, the population extending to Line 90 was only 19.3% of that in Line 70, and the one reaching Line 120 was only 1.7%. In August-September, the population reaching the Lines 90 and 120 was 10.4% and 1.3% of Line 70, respectively, and in November-December, 13.3% and 0% of Line 70 reached to Lines 90 and 120, respectively (Table D).

A generalized pattern of the distribution of *S. scrippsae* was obtained by averaging the number of specimens at each 25 m depth interval from 0 to 600 m for all seasons (Tables C and D). The highest concentrations occurred at level 100-75 m on Line 70, and at level 225-100 m on Line 90 and Line 120. The highest concentration of the population of *S. scrippsae* occurred on Line 70, of which only 16% reached Line 90, and 0.7% to the Line 120. Stations 70.60 and 70.110 had the highest average number of specimens, with no strong difference between them. On Line 90, the average population appeared more concentrated at Station 90.60, and at Station 120.55 on Line 120.

The data show that mortality, as indicated by the structure of the populations, is greater from spring through fall than in winter. Comparison of the present data for the upper 100 to 0 m with previous data off California for the seasonal cruises during 1954 and 1958 (Alvariño 1962, 1965a) indicates that the California Current was weaker during 1969 than in 1954, but stronger than in 1958.

The main southward flow of *S. scrippsae* populations, as shown by its abundance, was at Stations 70.75 and 90.60 in February-March 1969; at 70.75, 90.60, and 120.70 in May-June; and at 70.75, 70.110, 90.60 and 120.55 in August-September. At this time it reached its highest abundance in a large area, extending both deeper and farther west and south than during any other season of 1969. For November-December (with collections missing from several Stations), the flow extended along Stations 70.60 and 90.60.

The total number of tows were about the same for the combined seasons of spring and summer (578 hauls), and fall and winter (422 hauls) although those in winter cannot properly be compared with the other cruises. The numerical difference for both seasonal groups may not have statistical significance.

The present data show that *S. scrippsae* generally inhabits depths between 25 m and 475 m, and occurs occasionally below that deeper level off California. It appears more abundant in the two strata between 350 and 100 m, gradually decreasing in abundance and in the area size inhabited above and below those combined strata. In February-March, *S. scrippsae* came closer to the surface layers than during any other season, appearing in the 25 to 0 m stratum.

As expected, there is not a real remnant population of *S. scrippsae* restricted to the deep layers of the California waters during the winter months. However, the 1969 cruises covered only the southernmost portion of the distributional range of *S. scrippsae* along the northeast Pacific. The sampling, therefore, did not extend far enough west off California and north of San Francisco to give a complete picture of the distribution of the species. In previous studies (Alvariño 1962, 1964, and unpublished data), it was observed that all life Stages of the population were present north of San Francisco and in the Transition region band. Thus, locations north of San Francisco are strategic for the determination of the population structure of *S. scrippsae* entering the northeast Pacific flow of the California Current. The above analysis, of the distributional pattern presented by *S. scrippsae* off North America, indicates that the California Current population came from a northern source, sinking while progressing southwards. There remained the question as to whether the population could remain during the winter months in strata deeper than those reached by the oblique tows. The stratified hauls obtained in 1969 off California were used to determine the depth range and seasonal distribution of this species, and the results are presented here.

The depth ranges of the hauls for the collections in this study do not coincide with those of former CalCOFI collections, which were made with a one-meter net in oblique tows to various depths as follows: from 1940 to 1950, with 100 m of wire out (to 70 m deep); from 1951 to 1968, with 200 m of wire out (about 140 m deep), and from 1969 on, with 300 m of wire out (about 210 m deep). The plankton collections for 1954 and 1958 in the California Current region, which included integrated samples (oblique tows) generally from 0 to 140 m depth and, on a few occasions, to 400 m, were analyzed (Alvariño 1965a). In some instances *S. scrippsae* was present in the deep hauls, but it was not observed in the upper 140 m. However, a comparison of the catches of *S. scrippsae* obtained with Bongo nets during these studies, shown in Table C, includes standardized and average combined day and night number of specimens obtained per Station and season at the 25 m intervals. These data indicate that the largest numbers were usually obtained in the 225 to 100 m stratum. The data in this study indicate that while *S. scrippsae* appears in small numbers in the upper 100-m, the bulg of the population extends below those levels. Therefore, the CalCOFI standard hauls of 140 m depth could have not sampled most of the *S. scrippsae* population.

No adequate reproduction needed to build up the population of *S. scrippsae* in the California and Baja California region was observed to take place at Lines 70, 90, or 120. It is therefore evident that, as the population of *S. scrippsae* drifts southward off California, it encounters environmental conditions which apparently are not conducive for its survival, and so gradually decreases in numbers until it disappears.

PHSICO-CHEMICAL ENVIRONMENT

There is no clear evidence that physico-chemical factors such as temperature, salinity, and oxygen, or the presence of other populations such as phytoplankton blooms, might affect the population densities of *S. scrippsae.* The pattern of distribution of *S. scrippsae* shows a certain coincidence with the profiles of isohalines and oxygen isopleths. However, it appears that the environmental condition off California are not suitable for the normal spawning, growth and survival of this species inasmuch as only a few young and fully mature specimens were collected. It is known that the bulk of the population sinks with the isothermal waters it inhabits in its progression southwards. In the Transition region, which is the proper habitat for this species (Alvariño 1962, Kotori 1976, and personal data from URSA MAJOR for August-October 1965, ZETES for January 1966 Expeditions, and in the California region) *S. scrippsae* appeared in waters between 5°C and 12°C. Therefore, this species inhabits deeper strata off California than in its domain in the North Pacific, preferring waters of similar or closely-related temperature ranges. It is interesting to note that the peculiar wave-like distribution profile shown by *S. scrippsae* on Line 90 or cruise 6908-09, coincided closely with the isohaline profiles and oxygen isopleths (Figures 5, 6, 7, 8). However, in the locations where *S. scrippsae* sinks, the isotherms perform an inverse pattern, making an energence wave only in deep strata.

"High oxygen uptake" is a known characteristic of arctic lamelibranch species (Sparck 1936). Northern species displaced into warmer waters (Vernberg 1962) are known to increase their metabolic rates which may cause the animals to become deprived of food and oxygen. These factors may explain the high rate of mortality of *S. scrippsae* in the California region.

In February-March, the population of *S. scrippsae* extended up to the 75 m depth at Station 70.75 (Figures 1 and 5) coincident with the upper displacement of the deep isotherms. In May-June, upwelling of oxygen contours and downward displacement of isohalines on Line 70 (Figures 2 and 6) fit roughly the distributional pattern of *S. scrippsae.* In August-September, the upward of isohalines and oxygen isopleths and downward and upward distribution of isotherms on Line 70 and Line 90, correlated with the distributional features of *S. scrippsae.* However, the distributional pattern of upward displacement and sinking of *S. scrippsae* on Line 120 does not agree with any physico-chemical profiles for that Line of Stations on that cruise (Figures 3 and 7).

No explanation, however, can be made for the high concentration of *S. scrippsae* in the 600 to 475 m stratum at Station 70.60 in November-December for day and night collections (Figures 4 and 8).

It is interesting to note that this welling up and sinking of *S. scrippsae* appears similar to the particular vertical distribution pattern of *S. decipiens,* a mesopelagic Chaetognatha collected in day and night hauls during the same cruises and Line of Stations. This peculiar distributional feature might have been produced by the large eddy (Wooster and Jones 1970) formed by the warm deep undercurrent flowing northward off Baja California.

Northward reverse of the transport by the California counter-current (Reid 1962, 1963) could not be detected by the distribution of *S. scrippsae.* However, this counter-current flows closer to the coast than the waters usually inhabited by *S. scrippsae.* The population of *S. scrippsae* reached the southernmost extension mainly at the 600-350 m or 350-100 m depth strata; below those levels the population virtually disappears before reaching areas off Punta Eugenia, Baja California. Unfortunately no calculations of the geostrophic flow off California are yet available for 1969; these would be of values as "the drift of the plankon may be better estimated from the geostrophic flow than from the instantaneous current measurements" (Wyllie 1966).

Between consecutive day and night hauls, noticeable changes sometimes occurred in the vertical distribution of the species, while in other cases the bathymetric distributional pattern appeared similar or only slightly modified for both time and periods. Changes in the vertical distribution of the species at a location over so few hours could be due to variations in the environment caused by currents, eddies,

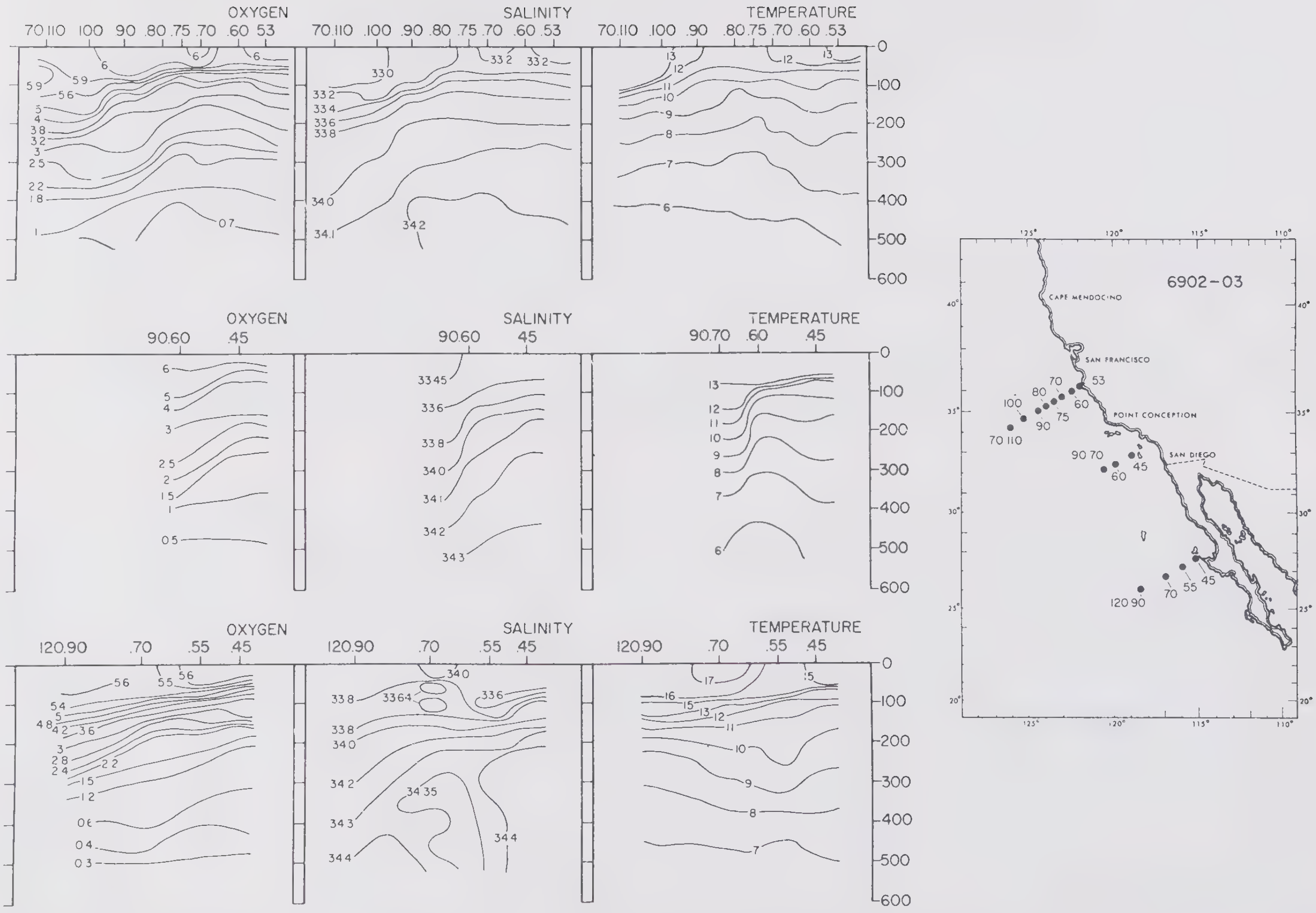

Fig. 5. Profiles of temperature, salinity, and oxygen for Lines of Stations 70, 90, 120, off California and Baja California, during February-March 1969 (6902-03), based on data University of California.

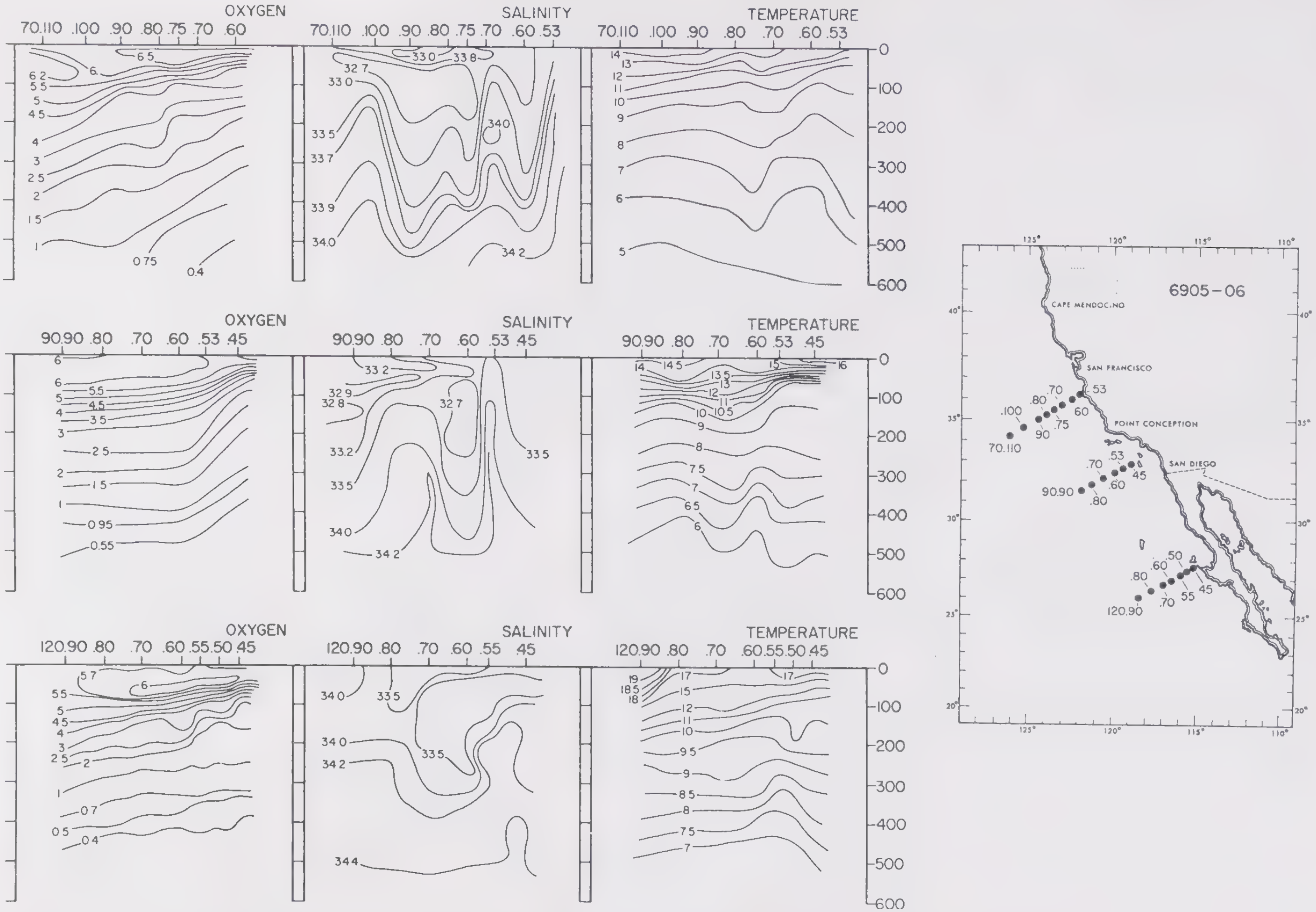

Fig. 6. Profiles of temperature, salinity, and oxygen for Lines of Stations 70, 90, 120 off California and Baja California, during May-June 1969 (6905-06) based on Data University of California.

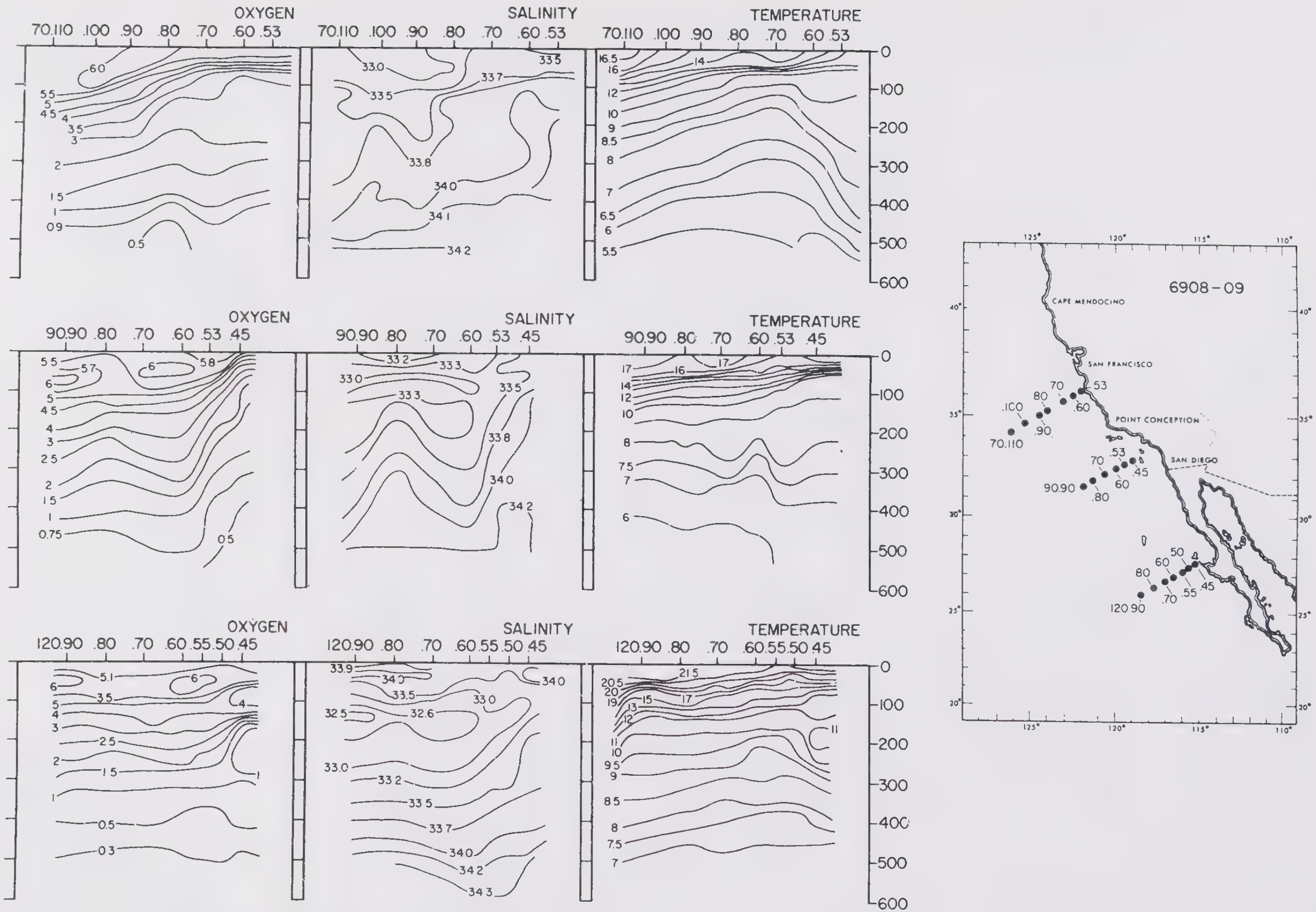

Fig. 7. Profiles of temperature, salinity, and oxygen for Lines of Stations 70, 90, 120, off California and Baja California, during August-September 1969 (6908-09), based on data University of California.

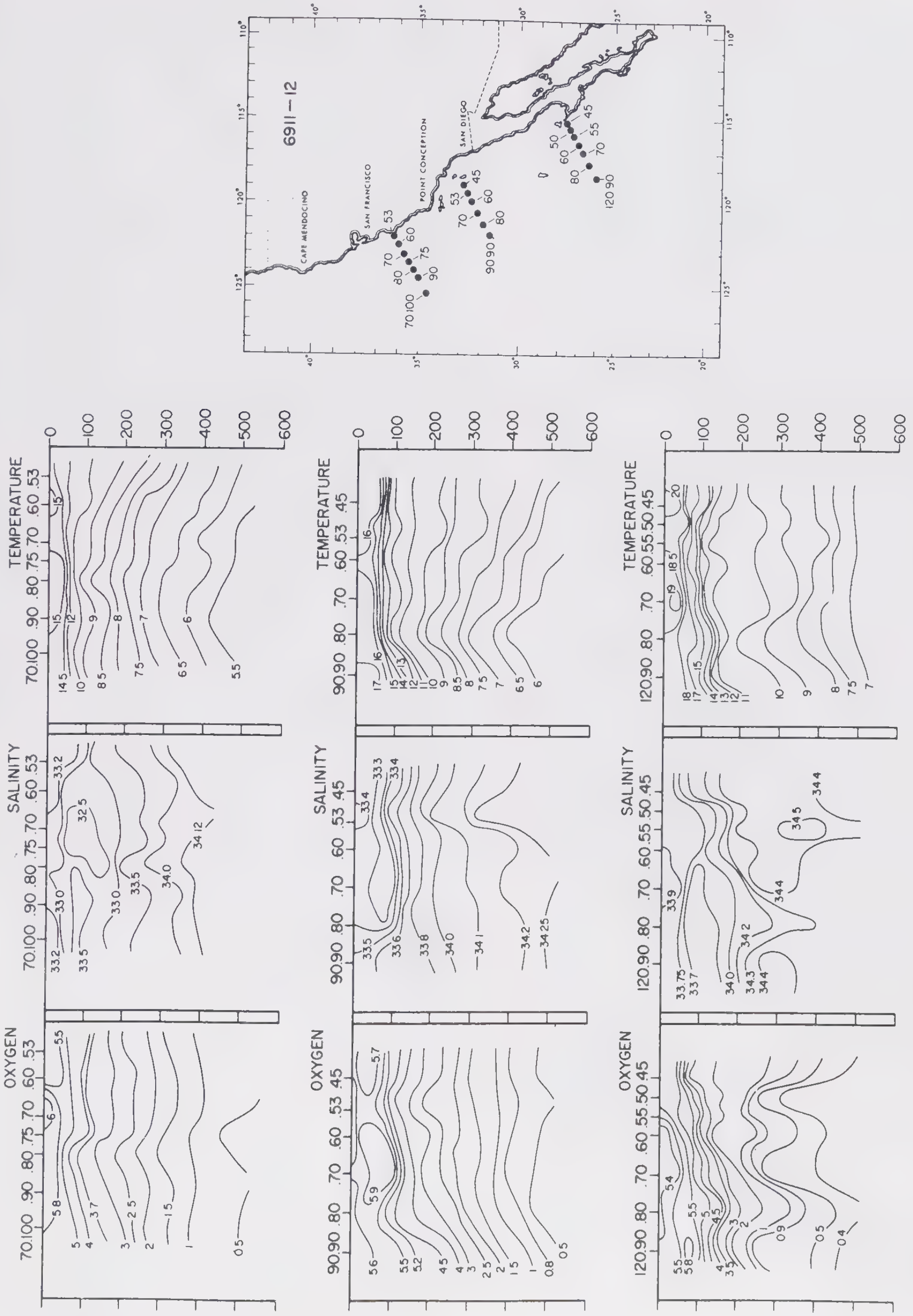

Fig. 8. Profiles of temperature, salinity, and oxygen for Lines of Stations 70, 90, 120, off California and Baja California, during November-December 1969 (6911-12), based on data University of California.

mixing processes, etc., bringing about either concentration or dispersal of the populations.

The fluctuations in the population density of this species may also be due to certain underdetermined favorable environmental factors, which are present in the Transition waters. The scarcity or absence of the species off California may suggest the absence of these favorable factors or the presence of environmental conditions unsuitable for the species' survival.

BIOTIC CONDITIONS AND DAY AND NIGHT DISTRIBUTIONAL PATTERN

Competition with other zooplankters whould be considered as a factor in determining *S. scrippsae* distribution. *S. scrippsae* inhabits the Transition region primarily with only two other species of Chaetognatha, *S. elegans* and *Eukrohnia hamata;* in the California waters, it occurs with more than 20 other species of this group.

The eastern distributional boundary of *S. scrippsae* off California is roughly correlated with the westernmost extension of *S. euneritica,* a typical neritic chaetognath of the North American Pacific (present data and Alvariño 1965a). *S. euneritica* mainly inhabits the upper 100 m or 75 m, while *S. scrippsae* extends to layers below those levels. A comparative analysis of the vertical distribution of *S. scrippsae* and *S. euneritica* off California showed that where *S. euneritica* was abundant, few or no *S. scrippsae* were present. In February-March 1969 at Station 70.60, *S. euneritica* appeared abundant at the 75 to 0 m and the 260 to 200 m strata, with no *S. scrippsae* at those levels. It appears that *S. scrippsae* and *S. euneritica* inhabit different ecological environments, and the presence of *S. euneritica* may delineate the eastern boundary of *S. scrippsae* distribution off North America. Similarly, it was observed that the presence or abundance of *S. enflata* off California (information collected during the study of the collections for 1969) coincided with only scattered specimens of *S. scrippsae.*

Differences in type, quality, and quantity of food in the Transition and the California regions should also be taken into account. Large concurrences of *S. scrippsae* (zooplankton predator) may be the result of an attraction to a concentration of food, and scattered numbers the reaction of the population to capture by predators: the typical behavior of predatory and prey organisms (rapid dispersal and sudden concentration). Decrease in numbers might also be due to increases in predation on these animals. If this is the case, distribution of predators (mainly fish and squids) of this species may have some bearing on the resulting distributional pattern. The data also indicate that some avoidance of the nets was taking place in daylight, with the larger specimens escaping by dodging the nets.

Differences in the bathymetric distribution could be due to the seasonal effects of spawning. Breeding, however, does not appear to have been restricted to any particular season, since collections from different seasons had similar population structures. Thus, it is likely that differences in the diel vertical distribution might be brought about primarily by water movemetns, wherein water may be replaced at the Station location by waters with more dense or more scattered populations.

Diel migration was shown to take place in some cases: some upward migration was observed at night in some instances, while in others upward migration appeared during daylight hours. However, there were some individuals which, remaining in the upper layers during daylight, may produce the resulted increase in the numbers captured in daylight hauls. The permanence of concentrated *S. scrippsae* in the upper layers during daylight may have been due to cloud cover, water turbidity or availability of food. The corresponding effect on the pattern of behavior of the animals, and the decrease in light intensity which influence the phototactic reaction of the animals, affected their vertical distribution pattern.

LIFE STAGES AND THE STRUCTURE OF THE POPULATION OF SAGITTA SCRIPPSAE OFF CALIFORNIA AND BAJA CALIFORNIA

Little is known of the life history of Chaetognatha, except for studies on *S. elegans* by Clarke, Pierce, and Bumpus (1943), Dunbar (1940, 1941, 1962), Huntsman (1919), Huntsman and Reid (1940), Kotori (1976), McLaren (1966), Redfield and Beale (1940), Sameoto (1971, 1973), and Sherman and Schaner (1968): on *S. hispida* by Reeve (1970); on *S. crassa* by Murakami (1959); on *S. nagae* (Nagasawa and Marumo 1978); and on *S. elegans* and *S. setosa* by Pierce (1941), Russell (1932a, 1932b, 1933a, 1933b), and Wimpenny (1937).

To learn more about the population structure of *S. scrippsae* four Stages of maturity were considered (Alvariño 1962) in order to determine reproduction, growth, and survival of the species: Stage I, specimens up to 30 mm long (ovaries starting to appear, or reaching up to anterior end of posterior fins); Stage II, specimens 31 to 40 mm long (ovaries reaching to midlenght of anterior fins); Stage III, specimens 41 to 50 mm long (ovaries reaching to anterior third of anterior fins); and Stage IV, specimens 51 to 60 mm long (ovaries reaching to neck region, ova large and mature filling the ovaries). Stage I includes three size groups (10 mm or less, 11 to 20 mm, and 21 to 30 mm). Stages II, III, and IV include the 10 mm size groups from 31 mm to 60 mm as listed. There may, of course, be exceptions to this classification scheme. For example, specimens 51 to 60 mm long could appear in Stage III, and specimens 31 to 40 mm may be fully mature or at Stage IV.

From the observed conditions of the female gonads, there appears to be only one maturity cycle in this species. Prontandry is strong, with specimens as late as Stage II (39 to 40 mm long) having ripe seminal vesicles. Female gonads of the species are not ripe until the animal is more than 50 mm long, while the male gonads might go through several cycles of maturity in the life span of the animals. Evidence of this is shown in a large number of specimens up to 30 mm or 35 mm long which were at Stage I or II of maturity for ovaries and ova, while the tail segment was filled with sperm and the seminal vesicles were full or bursting. The fact that female gonads require a great deal more time than male gonads to reach maturity, may be explained by the metabolic activity required to fully develop the female gonads and gametes. This activity consumes the reserves of the organism to such degree that, after maturity and spawning, the animal cannot recover and so dies. At the same time, there is evidence that male and female sexuality are separated in time for the same individuals; i.e., the hermaphrodite animals act first as males and later as females. Whit cross fertilization, the sperm is stored in the seminal receptacle of the ovaries of each of the coupled animals. Sperm reach the ripe stage to fecundate the ova at the time of spawning, when the female gametes are mature.

Ovaries reach the neck region in the fully mature individuals (approaching 60 mm long). The ova are arranged in four rows (data from present studies and other previous analyses by the author, and Alvariño 1962). The total number of ova per individual ranges from 700 to 1000. The length of each ovary ranges from 32 to 40 mm, reaching 48 mm in the largest individuals.

The average number of ova in mature specimens can be used to determine egg production and the apparent mortality at each stage of growth, and optimum conditions for reproduction, growth, and survival of the population in the species' domain and along the margins of its distributional range. To accomplish this, data from the main distributional region are needed. However, with the data at hand, it appears that the highest mortality rate occurred in the smallest size group, based upon de numerical magnitude of that part of the population of *S. scrippsae* in relation to the high number of eggs the mature individuals presumable release. Tables E, F, G.

It was found that *S. scrippsae* are present all year round in the Transition region of the North Pacific (the most stable domain of the species) where most reproduction takes place. Here the complete structure of the *S. scripp-*

sae population is present, from large fully-mature, to young newly-hatched individuals (author's personal data, Alvariño 1962, 1964, 1966; Kotori 1976). The whole population structure is also represented in the northernmost location of the surveyed area, the region which approached, but is not close to, the main distributional domain of *S. scrippsae.* The number of mature individuals decreases progressively southward until the only ones present, as determined from these collections, are specimens at advanced Stage I of maturity. In the California waters, only a few very young and a few large mature specimens were occasionally observed in the northernmost part of the surveyed region. However, the structure of the population of *S. crippsae* in its main distributional region (where it reproduces), has not been thoroughly studied.

In the region surveyed off California, two phenomena are superimposed: the biological season, spring-summer, when the major spawning occurs, and the maximum flow of the California Current coincident with that season, which conveys the population of *S. scrippsae* southrwards.

In addition, data on the population structure obtained in port and sparboard samples for each haul, and the size of the individuals obtained in each net, shown evidence of patchiness, which could possibly be the result of the animals avoiding the net (Alvariño 1967).

Stage I (including animals more than 10 mm in length) was present throughout the year, indicating that *S. scrippsae* spawns all year round in the Transition region and is brought into the California region with the flow of the California Current. Stage I specimens made up 90% of the population collected for each season of the sampling period. Stage II was also present throughout the year, but only a few specimens of Stage III. Some specimens of Stage IV appeared precociously mature, and were obtained off California in May. These were collected at 350-225 m adn only at night. Ontogenic stratification was observed, both bathymetrically and latitudinally, with the largest specimens appearing deeper and at the northernmost locations. The population fluctuation of this species is undobtedly related to changes in the California Current.

Considering the rate of drift and the life-span of the species, representatives of Stages II, III, and IV would be expected at the southernmost locations off California and Baja California. However, only specimens at Stage I were obtained. It could be suggested that some population replacement may occur locally, but this should be considered with caution because practically no fully-mature nor newly-hatched specimens were collected in those regions. The fact that only Stage I specimens were observed at the southernmost locations of the surveyed region indicates that the conditions may not be suitable to the survival of the species, and the surviving specimens may experience an arrest in their normal development.

The abundance and size distribution range of *S. scrippsae* off California during day and night are presented in Tables E, F, and G, and Figures 9, 10, 11, 12 and 13.

VERTICAL DISTRIBUTION OF MATURITY STAGES

Specimens less than 6 mm in length were not observed in the surveyed region. Specimens less than 10 mm (9 mm individuals) were found in May 1969 at night at the most oceanic Station on Line 70 at 50-25 m and 75-50 m depth at Stations 70.90 and 70.110, respectively. In August 1969, specimens 9 mm in length appeared at Station 70.90, and 6 mm to 9 mm specimens were found at Station 70.110 in both daylight and at night. These small specimens were observed at 50-25 m and 225-75 m during daylight, and at 100-75 m and 225-100 m at night, being more abundant at night than during daylight hours. In September, five specimens 9 mm in length were obtained at Station 120.55 during a night haul at 225-100 m depth (Table E).

These data suggest that, in summer, spawning may extend into California waters, although the bulk of reproduction takes place north of Line 70. The production of young from that source is so large that some individuals are able to reach the surveyed region and survive there. Slight and occasional spawning may oc-

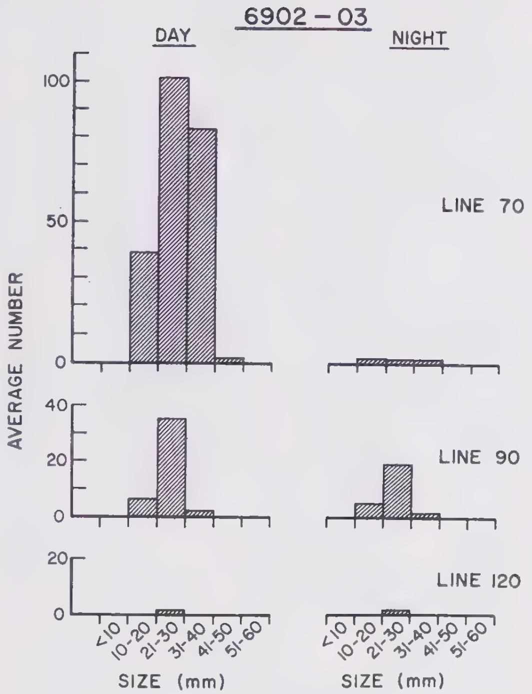

Fig. 9. Average day and night distribution of size groups of the population of *S. scrippsae* on Lines 70, 90, 120, off California and Baja California, during February-March, 1969.

cur in the surveyed region, as indicated by the very young individuals obtained off Punta Eugenia. The fact that small specimens (6 mm long) reached the Stations on the northernmost surveyed Line suggests that gravid individuals were present close to that region in August, having been brought there by the strong flow from the northern waters during that season, and that only slight (almost nil) spawning can be considered taking place from Line 90 southwards.

The largest size group of specimens (more than 50 mm long) were found only at Station 70.60, where five individuals 52 mm long were obtained in a night haul from 350-225 m depth.

SEASONAL DISTRIBUTION OF MATURITY STAGES

During February-March 1969, the largest number of individuals during daylight and night hauls (size group 21-30 mm) appeared on Line 70, with decreasing abundance for the 31-40 mm, 10-20 mm, and 41-50 mm groups, the most abundant group, 21-30 mm, was also most numerous on Line 90, for both daylight and night. It was also the only size group represented at Line 120. However, the second most abundant group on Line 90 was 10-20 mm for both daylight and night, while group 31-40 mm (which was second on Line 70) was scarce, and group 41-50 mm was absent.

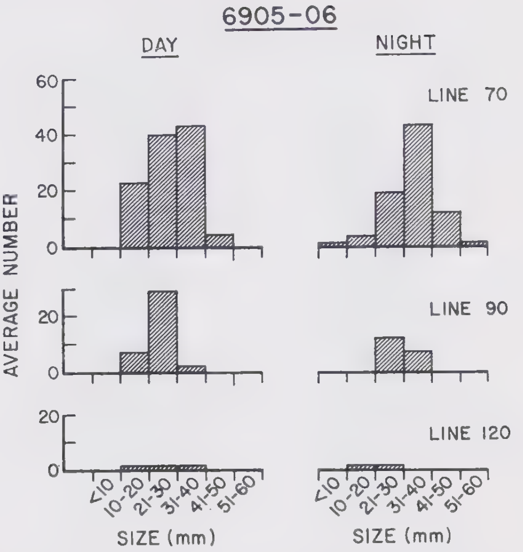

Fig. 10. Average day and night distribution of size groups of the population of *S. scrippsae* on Lines 70, 90, 120, off California and Baja California, during May-June, 1969.

During May-June, the highest average number of individuals occurring day and night on Line 70 belonged to size group 31-40 mm, followed (in decreasing abundance) by groups 21-30 mm, 10-20 mm, and 41-50 mm at daylight, and groups 21-30 mm, 41-50 mm, 10-20 mm, 50-60 mm and less than 10 mm at night.

During the summer, the highest average number of individuals on Line 70 was from size group 21-30 mm, followed (in decreasing abundance) by size groups 10-20 mm, 31-40 mm, less than 10 mm, and 41-50 mm. During night hauls, the most abundant size group was 10-20 mm, followed by size groups 21-30 mm, 31-40 mm, less than 10 mm, 41-50 mm. How-

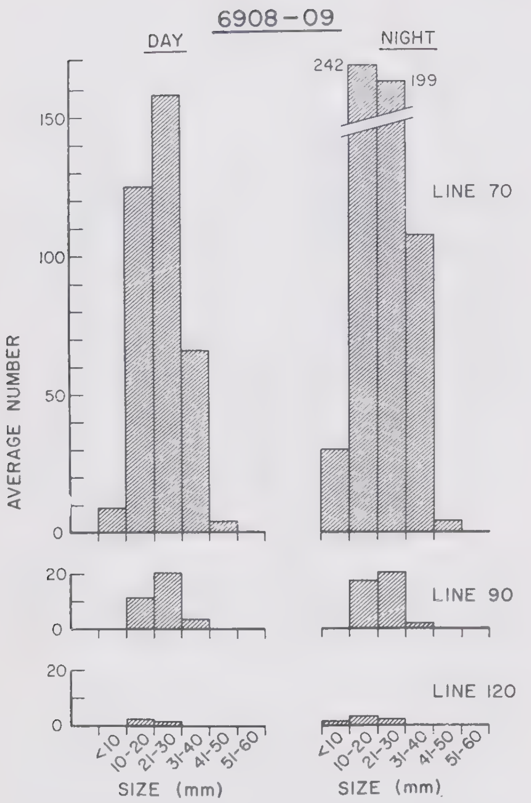

Fig. 11. Average day and night distribution of size groups of the population of *S. scrippsae* on Lines 70, 90, 120, off California and Baja California, during August-September, 1969.

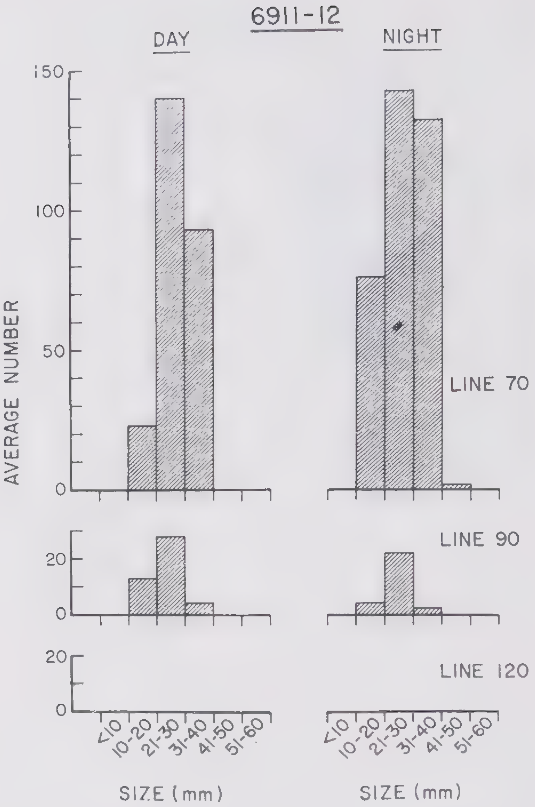

Fig. 12. Average day and night distribution of size groups of the population of *S. scrippsae* on Lines 70, 90, 120, off California and Baja California, during November-December, 1969.

ever, the most abundant size group on Line 90, both day and night, was 21-30 mm (the most abundant group at night on Line 70), followed by 10-20 mm and 31-40 mm size groups. The remaining size groups were missing. On Line 120, the most abundant group was 10-21 mm, followed by 21-30 mm for both daylight and night. During the night hauls, five specimens 9 mm in length were obtained (indicative of an occasional slight spawining in the area). The sharp difference in the range of size groups observed for daylight and night hauls during the spring was not evident in the summer.

During the fall, the most abundant size group on Line 70 was 21-30 mm, followed by size groups 31-40 mm and 10-20 mm for both daylight and night, and 41-50 mm at night. Specimens collected at 600-475 m at Station 70.60 ranged from 15 to 38 mm in daylight and 11 to 38 mm at night, with modes of 27 mm and 21 mm, respectively. Size group 21-30 mm was also the most abundant on Line 90, followed by the 10-20 mm and 31-40 mm groups. No representative of *S. scrippsae* reached Line 120 in the fall. There was also a wider range of size groups at night than at daylight during the fall. This phenomenon was not evident during winter and summer but was obvious during spring and fall when the turnover of biological and climatic periods occurs.

On the whole, a wider range of size groups were captured during the night hauls than the

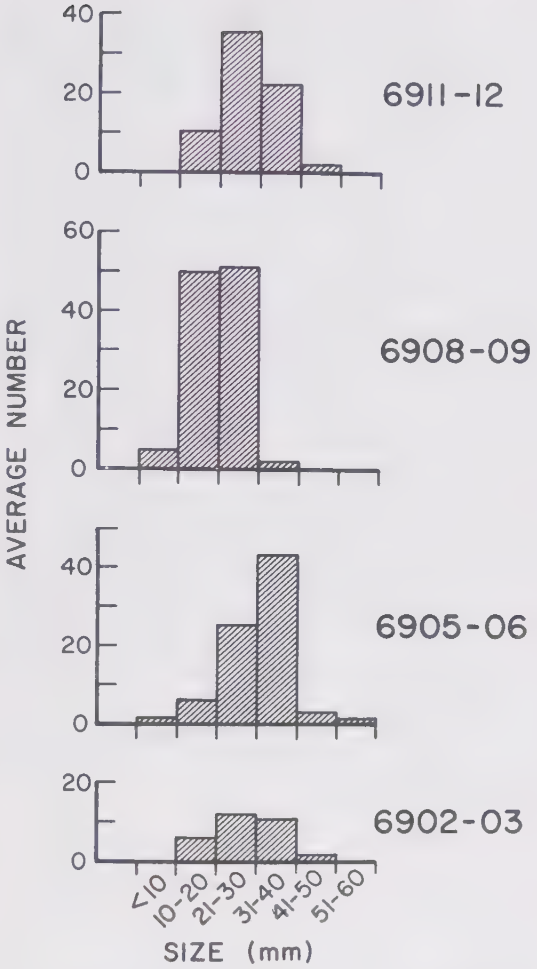

Fig. 13. Average size distribution (day and night combined) of *S. scrippsae* off California and Baja California during the four seasons combined of 1969.

daylight. The animals' behavior varied from night to day, being more alert to vibrations produced by the approaching net during daylight than at night, indicated by the size ranges obtained during both daily periods. Groups at both extremes of the size range appeared less abundant during daylight than at night.

The structure of the population of *S. scrippsae* in the uppre 100 m during 1969 was analyzed to compare it with the population obtained in the standard 1954 and 1958 CalCOFI cruises. The population collected in the upper 100 m in the present studies included specimens ranging from 12 to 38 mm in February-March, 9 to 45 mm in May-June, 6 to 45 mm in August-September, and 10 to 38 mm in November-December. Specimens 44 to 45 mm long were occasionally obtained at 100-0 m levels during May and August 1969. These data and my unpublished notes on the sizes of *S. scrippsae* collected in the monthly cruises off California during 1954 and 1958 indicate that large mature specimens are virtually absent from the upper 100 m in this region, and that Bongo nets capture larger individuals than the one meter CalCOFI nets. The one meter net is therefore not adequate for collecting *S. scrippae;* Bongo nets without bridles are more effective.

Although growth rates are known for *S. hispida* (Reeve 1970) and *S. gazellae* (David 1955), the closest relative of *S. scrippsae,* there is no knowledge of the growth rate of *S. scrippsae* because no studies have been made of its population structure in the main area of its distribution (i.e., the Transition region band of the North Pacific). Growth rates may vary for the different sized individual, being higher for the young, and progressively decrease with increasing length. When development of the gonads occurs, food intake is increasingly channeled to this activity, with a proportionately decreasing amount given to body growth.

The disappearance of fully mature individuals may be due to their inability to survive under adverse conditions. When the whole population declines, large mature individuals will occur in such small numbers that there will be little chance of their being represented in the collections.

The consistently low percentage of the size group less than 10 mm long throughout the four surveys is remarkable, and may be due to several factors. The relatively rapid growth rate of the animals in the youngest generation while reaching the medium size Stage I, for example, is a possible cause of the reduced number of specimens of that size in the population at any one time. Gear limitations should also be considered in the loss of the individuals at both extremes of the size range, although this phenomenon may apply more to the larger sized animals than to the very small ones.

The distributional domain of *S. scrippsae* is strictly bound to the Transition waters. Therefore, the temperatures or salinities encountered by this population off California should be adequate for spawning and survival of the species. However, practically no spawning took place south of San Francisco during 1969. Perhaps food quality or another factor inhibited sexual development. It has been considered that growth, maturity of the gonads, and production of ova or eggs, may be related to the characteristics of the food ingested. *S. scrippsae* devours every type of zooplankton (fish larvae, medusae, chaetognaths, copepods, euphausiids, and other crustaceans). Both the amount and quality of available food may be critical factors because this species is incapable of storing food reserves. Sameoto (1973) stated that food was not a limiting factor in determining the growth rate of *S. elegans* in the Bedford Basin, Nova Scotia, and also that growth was limited by the low temperature water. The present study does not support this statement.

Growth rate is retarded by lack of food or other unfavourable conditions in the natural habitat (Russell 1932a), and growth rate and maturity of the gonads are accelerated with increasing temperature (Bullock 1955). Some specimens of *S. scrippsae* were found to be retarded in sexual development; for example, 40 to 45 mm specimens normally corresponding to maturity Stage III appeared to be at Stage I or II. Such differences in the maturity of the gonads may be dependent on food and environmental conditions, which would account for an effect in the physiology of these animals.

Temperature may be relevant when other factors remain constant, such as food supply or certain undetermined environmental factors. In this study, although temperatures encountered in the strata inhabited by the species off California were similar or within the higher segment of its normal temperature range in its main distributional region, gonad development did not appear directly related to this variable. Growth rate should not have been retarded but enhanced by such temperatures; however, this was not the case, as seen in the retardation and failure of gonad development.

The few shorter specimens of *S. scrippsae* (35, 40, 41, and 45 mm long) at Stage IV of maturity (female gonads) obtained during May-June cruise, may have resulted from two possibilities: either those specimens encountered optimal conditions of food and some other factors, which, together with high temperatures permitted precocious development of the gonads, or, as observed by Reeve (1970) in laboratory studies on *S. hispida,* they experienced shrinkage in body length due to starvation, seemingly at Stage IV.

A few S. scrippsae observed had parasites (nematodes and tremetodes) in the body cavity. In these specimens, development of the ovaries was retarded: individuals more than 40 mm in length were at maturity Stage I. The lack of adequate food uptake may be one of the important factors responsible for the retarded maturity of this species.

An additional source of information on the distribution of *S. scrippsae* may be found in past records and studies done on some commercial fisheries. For example, Le Brasseur (1959) found that salmon catches in the northeast Pacific off Canada were inversely related to the oceanic flow as characterized by the occurrence of *S. scrippsae* (identified as *S. lyra*) into that region. This change in salmon catches, according to Le Brasseur, was found even at locations where change in physico-chemical characteristics was not detectable. It should also be noted that high catches of salmon in the northeastern Pacific coincide with low or nil catches of albacore, *Thunnus alalunga* (Powel and Peterson 1957). Evidence of positive correlation was observed between the distribution and abundance of *S. scrippsae* off North America and the albacore in these waters (author's unpublished date, Albacore Cruise 63, AO-7, June-July, 1971, R/V DAVID STARR JORDAN, NOAA, National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, California). It was further observed, when analyzing the distribution of the longline catches of albacore in the

Pacific (Alvariño 1970) that the fish were found in late September and in October in the northeastern part of the Transition region of the North Pacific waters, which might be their main westward migratory route. It has also been observed (Alvariño's unpublished data) that *Trachurus symmetricus* larvae survive better in waters inhabited by *S. scrippsae* off California.

With data from locations north of the area surveyed during 1969 cruises, it could be possible to follow the history of the broods of *S. scrippsae,* rate of growth, survival, interactions with other species, and their transport by the current, which would be of value in tracing the water movement and transport with time off California. The methods used to predict the spawning season in chaetognaths include: 1) Determining the number of individuals at early Stage I, and 2) Comparing the percentage of adults with ripe gonads to the percentage of young. The latter cannot be applied in the present study because the area investigated is only the southernmost extension of the species' distributional region. Information obtained during the various seasons in the Transition region include detailed observations on changes in the West Wind Drift flow, and the characteristics of eddies developing into the Central Pacific waters north of Hawaii. Comparison of these with Eber's (1971) hypothesis of standing waves in the current structure and changes in the characteristics and strength of the California Current through the years and seasons should provide necessary additional information. Wyllie (1966) reinforces the mentioned plan of study, implying that "the variation in strength of the California Current is probably controlled by the strength and direction of the West Wind Drift at the time it is influenced by the presence of the continent of North America." That information could provide answers and the clues needed to foretell the characteristics of the California Current, based on data collected in key location during the winter or early spring in the Transition region. This prognosis could be used to determine characteristics of fisheries in the North American Pacific.

Sagitta scrippsae could be used to rapidly detect the presence of the Transition waters off the California coast and the degree of mixing of those waters. This species can be identified easily in a plankton sample with the naked eye if necessary, even by a non-specialist, after a short training period.

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NECTOCARMEN ANTONIOI, A NEW PRAYINAE, CALYCOPHORAE, SIPHONOPHORA FROM CALIFORNIA

Angeles Alvariño

Abstract.—*Nectocarmen antonioi* n. gen., n. sp. was found 13 April 1981 at 33°36.7′N, 118°18.4′W, off California, at a depth of less than 70 m. The siphonophore was complete, with nectophores, gastrozooids, tentacles, palpons, tentilla, bracts, and gonophores. It differs from other genera (*Rosacea, Nectodroma* or *Praya, Prayoides, Lilyopsis, Desmophyes, Stephanophyes*) in the subfamily Prayinae in the characteristics of its nectophores, bracts, and gonophores, but constitutes a morphological link among them.

Nectocarmen, new genus

Diagnosis.—A member of the subfamily Prayinae, which includes the genera *Rosacea* (2 species), *Nectodroma* or *Praya* (2 species), *Lilyopsis* (2 species), and *Prayoides, Desmophyes,* and *Stephanophyes* (1 species each). The principal characteristics of these genera and of *Nectocarmen* are given in Table 1.

Type-species.—*Nectocarmen antonioi,* new species.

Etymology.—*Necto* ("swimming," Greek) + *Carmen,* my mother's name (Latin for poetry, song, and garden).

Nectocarmen antonioi, new species

Figs. 1–5

Material.—Off California, San Pedro Channel, 33°36.7′N, 118°18.4′W, R/V *David Starr Jordan* sta 88.3 *33,* cruise 8104, 13 April 1981, vertical tow from about 70 m to surface: Holotype, complete colony, USNM 60895; paratype, eudoxids, USNM 60896.

Etymology.—Named for my father, Antonio.

Description.—The subfamily Prayinae of the suborder Calycophorae are large prayids with pulsating nectophores and a heavy stem. The bracts are composed of a large amount of mesoglea, which aids the flotation of the whole animal. Prayids lack the apical gas-filled float of the Physonectidae, and are propelled by the nectophores at the upper part of the stem, which also supports the large bracts, gastrozooids, palpons, tentacles, tentilla, and gonophores.

The holotype is based on a polygastric specimen with a pair of small nectophores at the top of the stem, and well-developed eudoxids hanging from the stem, along with bracts, gastrozooids, tentacles, palpons, tentilla, gonophores, and free cormidia. The details of the siphonophore observed have been carefully reproduced, and the whole animal represented in detail in Fig. 1. Drawings give a more reliable representation of specimens than photographs.

Polygastric phase: In the polygastric phase, *Nectocarmen antonioi* exhibits 2 transparent kidney-shaped cylindrical nectophores, one slightly larger than the

Table 1.—Principal differential characteristics of the genera in the subfamily Prayinae, and the new genus.

Genera character	*Rosacea* Bigelow, 1911	*Praya* Quoy & Gaimard, 1833 = *Nectodroma* Bigelow, 1911	*Prayoides* Leloup, 1934	*Lilyopsis* Chun, 1885	*Desmophyes* Haeckel, 1888	*Stephanophyes* Chun, 1888	*Nectocarmen* n. gen.
Nectophores	Large flat smooth cylinders. Large hydroecium.	Round large pair with multi-form (branched) radial subumbral canals. Large hydroecium.	Round large pair, deep hydroecium.	3 equal size wedge-shaped.	Biserial lateral view wedge-shaped soft and transparent.	Distributed in corona.	Soft, transparent kidney shape. Hydroecium small deep groove.
Somatocyst	Does not lie as a free canal in mesoglea, but forms the pallial canal on dorsal wall of hydroecium.	Branched system of canals.	Unbranched short upper branch, or short descent branch and a short thick upper one.	Simple thin tube, lying obliquely in mesoglea.	Simple club ended, lying obliquely in mesoglea.	Complex asymmetrically rebranching up to ten times. Tips of branchlets pigmented.	Single, pear-shaped, lying vertically in mesoglea.
Nectosac	Small, about 1/4 of length of nectophore. Sinuous meandering lateral canals.	Small, ¼–½ of length of nectophore. Canals multi-branched or in network.	Short, branched canals, up to 15 branches.	Large, with meandering radial canals. Ostial tubercles or pigmented spots.	Small. Lateral radial canals straight. Ring of minute pigment flecks and tubercles around the ostium.	Occupying great part of nectophore. Ostium nearly parallel with long axis. Some small red tubercles on ventral side of ostium.	Large, occupying most of nectophore. Anterior and posterior canals straight, lateral canals reach up close to top of nectosac bending down to ring canal. No tubercles or pigmented spots on ostium.

Table 1.—Continued.

Genera character	*Rosacea* Bigelow, 1911	*Praya* Quoy & Gaimard, 1833 = *Nectodroma* Bigelow, 1911	*Prayoides* Leloup, 1934	*Lilyopsis* Chun, 1885	*Desmophyes* Haeckel, 1888	*Stephanophyes* Chun, 1888	*Nectocarmen* n. gen.
Bract	Oval, with central organ. Left and right hydroecian canal of different size (one less than ¼ of other) Dorsal bracteal canal short, extends to anterior part. Ventral bracteal canal short.	Flattened semicircular. No median central organ. Dorsal bracteal canal recurved. Ventral bracteal canal long. Both bracteal canals may have small branches. Hydroecial canals of almost equal length.		6 bracteal canals. No central organ.	Kidney shape, round above. With median pear-shaped vesicle (central organ). 4 main bracteal canals.	Bracteal canal system similar to previous genera.	Transparent, oval, flat. Bracteal canals almost straight. One hydroecial canal larger and more curved than the other.
Gonophore	Well-developed medusoids. No asexual eudoxid nectophore.	Medusoids with well developed radial and ring canals. ♀ larger than ♂. Pedicular canal trifid branched. Female with 4–6 large ova.		Large asexual eudoxid nectophores. Radial canals in 2 pairs from pedicular canal. Unisexual gonophores with reduced umbrella. Females and males on same stem.	Large asexual eudoxid nectophores, and groups of unisexual reduced gonophores. Eudoxids of both sexes on same stem.	Large asexual eudoxid nectophores, with meandering canals. The 4 radial canals do not branch together from pedicel. Small red tubercles. Bunch of reduced medusoid gonophores, canals in zigzag branching laterally. 2–3 female alternating with 2–3 male cormidia.	No asexual eudoxid nectophores. Gonophores laterally flat hemispheres, with 4 straight radial canals together from pedicel to ring canal. Pedicular canal trifid branched. Ovaries with small ova. No tubercles or pigmented spots on edge of umbrella.

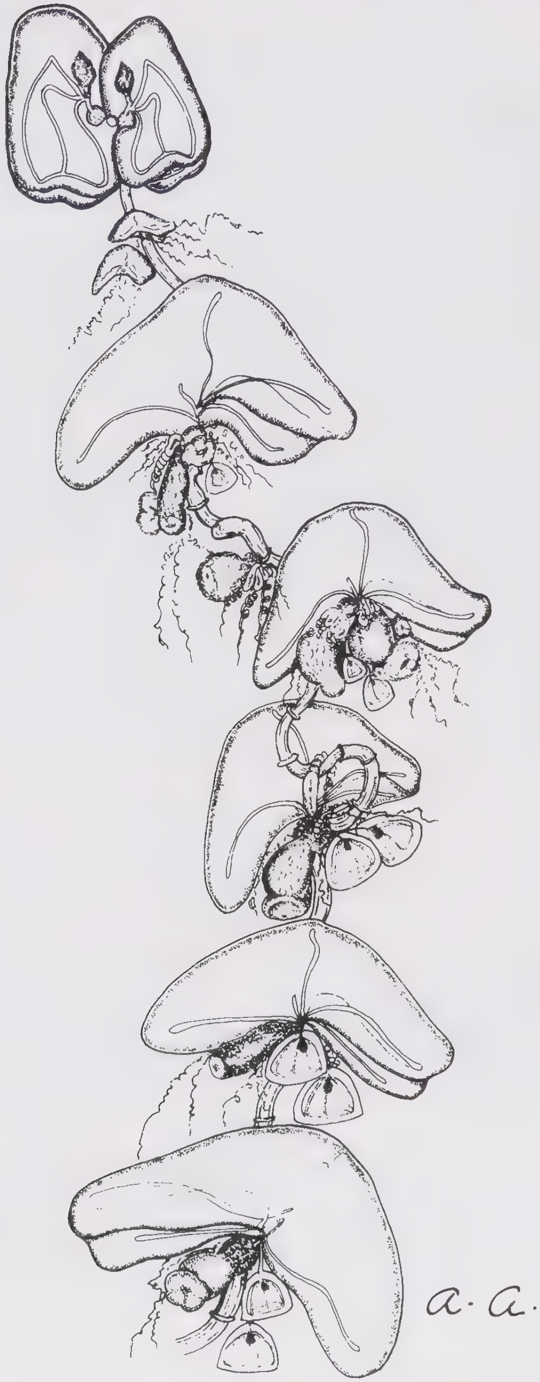

Fig. 1. *Nectocarmen antonioi*, complete specimen, about 200 mm long.

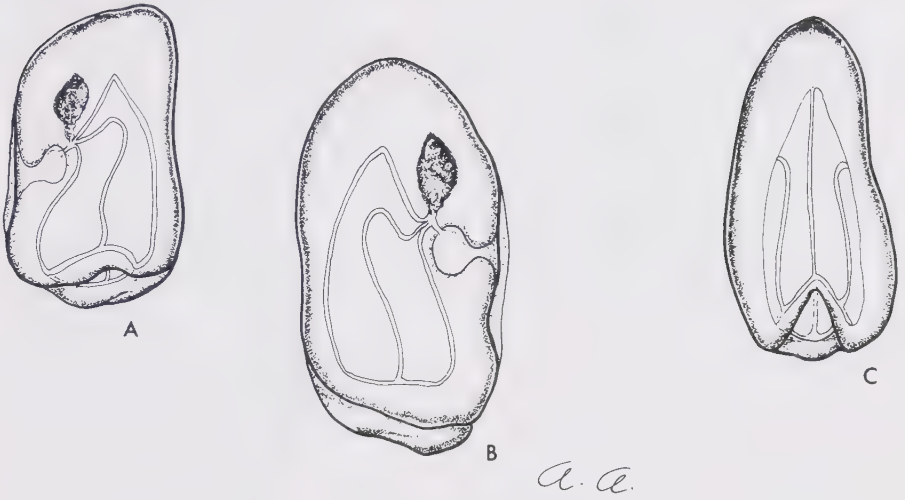

Fig. 2. Pair of nectophores of *Nectocarmen antonioi* (3–4 mm long): A, Small nectophore; B, Large nectophore; C, Dorsal view of either nectophore. Hydroecium, nectosac, radial and circular canals, and somatocyst can easily be observed.

other, with a large nectosac reaching nearly to the top of the nectophore. The nectophores are 3–4 mm long and about 2.5 mm wide. The hydroecium is only ⅓ the width of the nectophore, and does not run its entire length; it forms a deep groove, with rounded lobes (superior and inferior) closing the entrance, and this whole structure is covered by the flaps of the nectophore walls.

The pair of nectophores are bound together by the hydroecium, embracing each other by this structure (Fig. 2).

The nectosac is large, similar to that of *Stephanophyes superba* Chun, 1885 (1891) but with differences in the hydroecium, somatocyst, and radial canals. The pallial canal extends slightly up the nectosac, forming the radial canals. The anterior and posterior radial canals are straight, and the lateral canals bend upward to a position close to the top of the nectosac, then turn straight down to the ring or circular canal. The velar end of the nectosac, the ostium, is large, extending upward at the dorsal side. No ring of minute pigment flecks or tubercles is observed on the ostium.

The somatcyst is pear-shaped, and lies vertically in the mesoglea, extending slightly above the top of the nectosac.

Gastrozooids retain the larval tentacle, modified to form a series of tentilla. The base of the gastrozooids is enlarged into the nematocyst-producing area, the basigaster.

Palpons of reduced gastrozooids, with simple tentacles or palpacles, serve as feelers or testers.

The tentilla, with the subterminal battery of nematocysts, are spirally twisted filaments, with cnidobands (sabre-shaped nematocysts) forming the chief part of the stinging organs.

Gastrozooids, tentacles, palpons and tentilla lie under the bracts, and are shown in Fig. 1, and in detail in Fig. 3.

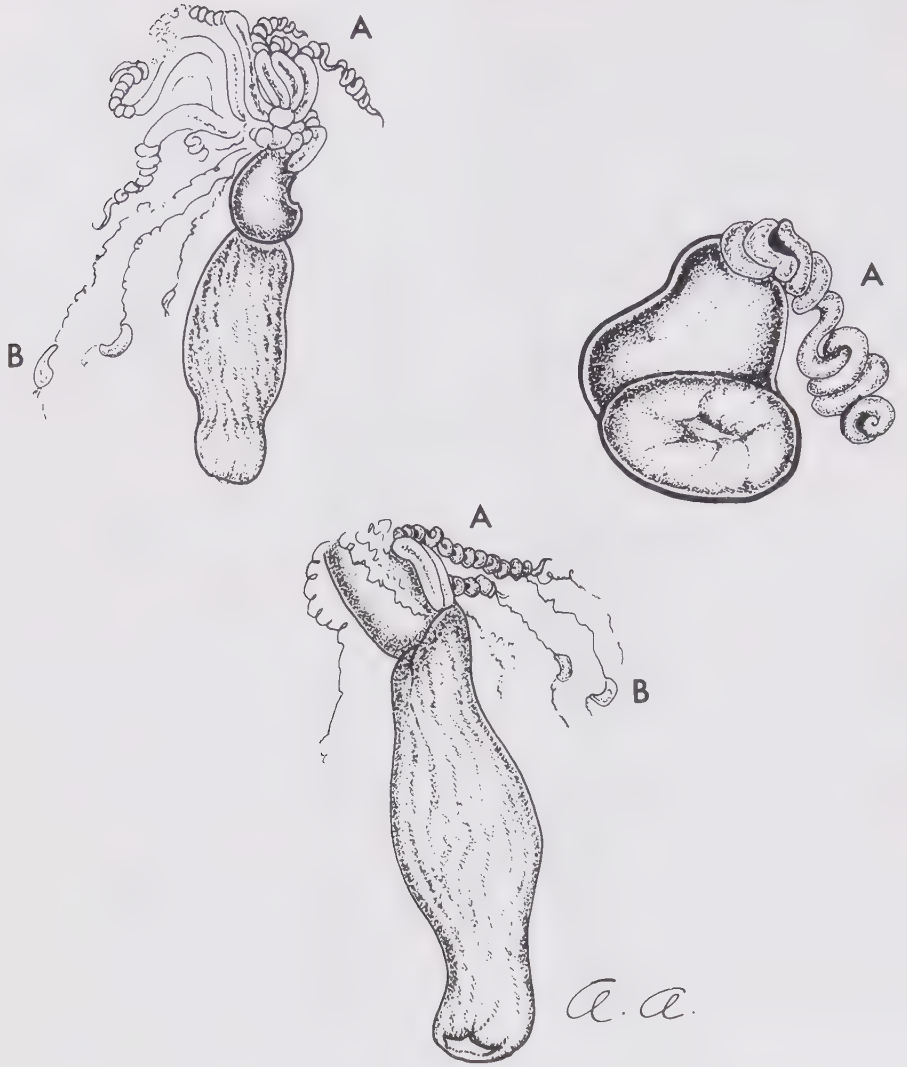

Fig. 3. Gastrozooids of *Nectocarmen antonioi* (2–3 mm long): A, Tentacles; B, Tentilla.

Eudoxid phase: The eudoxid phase has no asexual nectophore.

The bracts, which reach a maximum length of 10–12 mm, are oval, kidney-shaped, laterally flattened masses of mesoglea, the inferior part of which is concave and the upper part convex. They are divided into 2 lobes, with a third lobe on the concave distal side forming part of the hydroecial cavity of the bract. Unlike *Desmophyes,* no central organ (pear-shaped vesicle) is present at the junction of the main bracteal canals.

The bracts contain 4 large canals. The dorsal bracteal canal, which is slightly curved, ends in an ampullar dilatation, as does the nearly straight ventral bracteal canal; left and right hydroecial canals also end in ampullar dilatations. The right

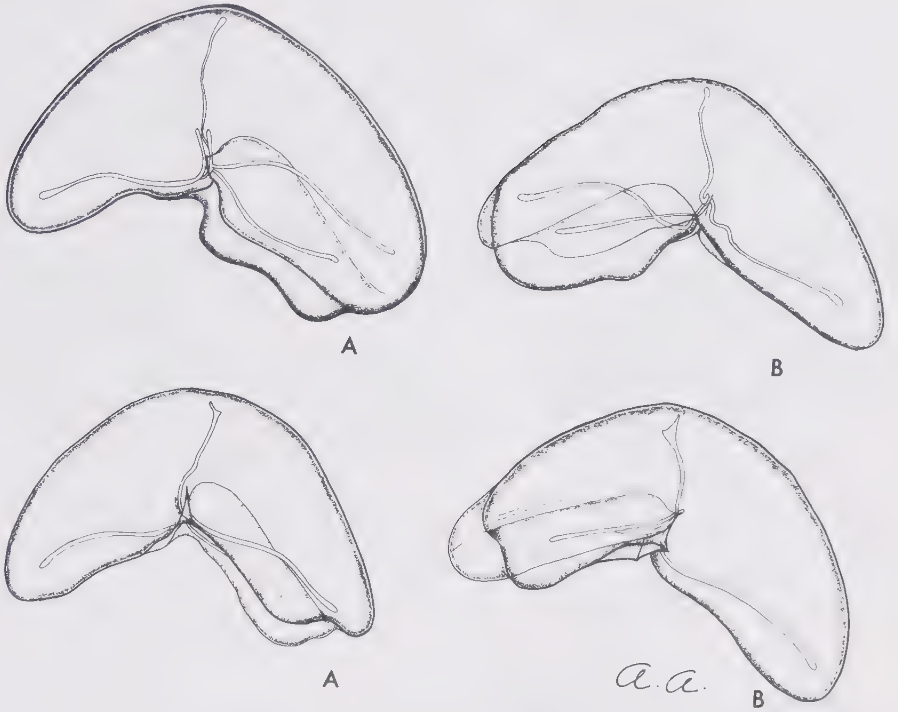

Fig. 4. Bracts of *Nectocarmen antonioi* (10–12 mm longest axis): A, Lateral right view of two bracts; B, Lateral left view of two bracts.

hydroecial canal is longer than the left. The former curves upwards and then extends down, and the latter bends down and then up. Usually, the left canal is straighter than the right. Neither the bracteal nor the hydroecial canals branch into small branchlets or spurs (Fig. 4).

The bracts, with gastrozooids, tentacles, palpons, tentilla and gonophores, may detach from the stem and swim freely in the ocean.

The sexual gonophores are large and hemispherical in shape, laterally flattened, retaining the medusoid characteristics, but without marginal tentacles. Female and male gonads occupy the mouthless manubrium. The gonophores pulsate intermittently, and are capable of propelling the cormidia in the water.

The gonophores are budded at the stem, below the base of the gastrozooids. They are, as explained, large bells, laterally compressed, with 4 straight radial canals ending at the ring canal. The bells hang from the bract by the pedicular canal, and the four radial canals run from the pedicel to the circular canal. Near the top of the umbrella, the pedicel has trifid branches embedded in the mesoglea, as is seen in *Nectodroma (Praya) reticulata* (Bigelow, 1931). The large, pear-shaped vesicles inside are the female gonads, containing numerous small ova. Male gonads are small, pointed, sausage-shaped vesicles (Fig. 5).

Male and female eudoxids may be found on the same stem.

It is probable that each cormidium includes either male or female gonophores, providing a sexual separation when male cormidia and female cormidia swim

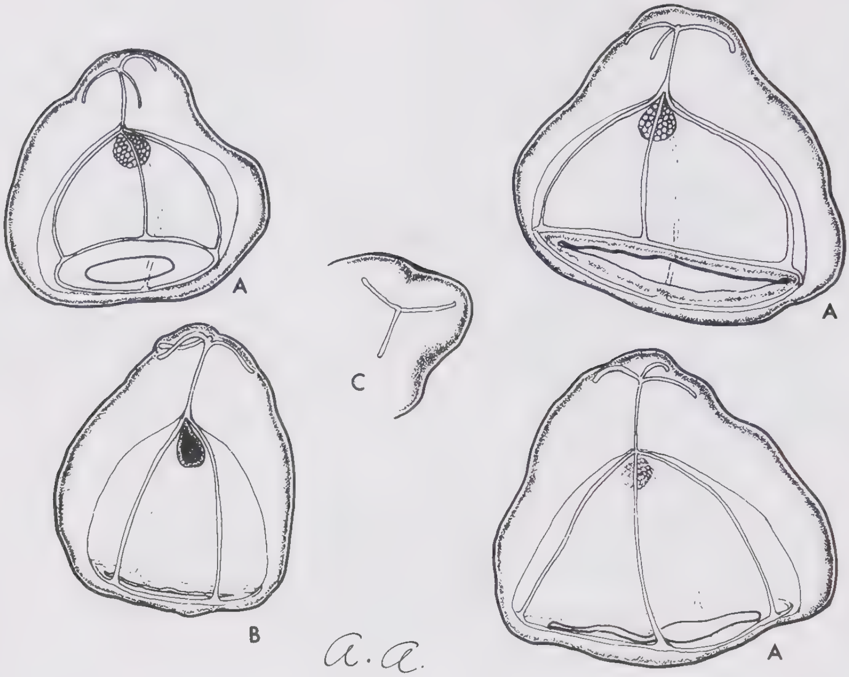

Fig. 5. Gonophores of *Nectocarmen antonioi* (3–4 mm high): A, Female gonophores; B, Male gonophore; C, Upper view of gonophore to show the trifid branching pedicel.

freely in the ocean. Some of the cormidia were detached, but obviously belonged to the same whole animal.

The nectophores, bracts, and gonophores are transparent; gastrozooids, palpons, and tentacles range in color from bright reddish to faded pink or rose.

The nectophores function in propulsion; the bracts are composed of enlarged masses of mesoglea and act as protection for gastrozooids and gonozoids or gonophores, as well as contributing to the buoyancy of the animal. The stem contracts and expands, and the gonophores also perform active pulsations, contributing to the propulsion of the siphonophores; by spreading the stem into loops they also amplify the potential field of the tentacles and the fishing predatory capacity of the siphonophore.

Discussion.—The principal differential characteristics of the genera in the subfamily Prayinae are presented in Table 1, together with those for *Nectocarmen* n. gen.

The general shape of the nectophores is similar to that of the other genera in the subfamily, especially *Rosacea* Bigelow, 1911, and *Desmophyes* Haeckel, 1888, also described by Kawamura (1915). However, the hydroecium is smaller than that of *Rosacea,* or *Desmophyes,* and similar to that of *Stephanophyes.* The nectosac is large, as in *Stephanophyes* and *Lilyopsis* (Alvariño 1981; Chun 1885, 1891), but the radial canals do not display the meandering pattern observed in *Stephanophyes* and *Lilyopsis.* The somatocyst of *Nectocarmen* is different from that of other Prayinae genera, including *Prayoides intermedia* Leloup, 1934.

The bracts resemble in general outline those of *Nectodroma (Praya)*, but differ in the detail of the shape and pattern of the canals, as can be observed by comparing present illustrations with those by Alvariño (1981), Bigelow (1911), and Totton and Bargmann (1965). Bracts in *Nectocarmen antonioi* do not have the vesicular organ of *Desmophyes*.

The eudoxids of the new siphonophore do not have the large asexual eudoxid nectophore that is found in *Lilyopsis*, *Desmophyes*, and *Stephanophyes*. The gonophores are similar to those of *Nectodroma (Praya)*; however, sexual nectophores are pear-shaped in *Nectodroma*, and hemispherical in *Nectocarmen*. Both *Nectodroma (Praya)* and *Nectocarmen* present the trifid branched pedicular canal, but the gonads of the former include 4–6 large ova (Bigelow 1931), while in the latter the ova are small and numerous. In *Nectocarmen* the four radial canals of the gonophore converge at the pedicel, and run straight to the circular canal, characteristics different from the other genera in the subfamily, though similar to *Nectodroma (Praya)*. No tubercles or pigmented spots appear on the margin of the gonophoral umbrella, whereas in the other species of the subfamily those structures are present.

Species of the following Prayinae have been observed in California waters (Alvariño 1967, 1971): *Nectodroma dubia* (Quoy and Gaimard, 1833), *N. reticulata* (Bigelow, 1911), *Rosacea plicata* Bigelow, 1911. Bigelow and Leslie (1930) reported *N. reticulata* from Monterey, but Totton and Bargmann (1965) indicate it was probably *N. dubia*.

There is a peculiar phenomenon common to Siphonophorae and Medusae, in that most of the species present an erratic distribution (Alvariño 1977, 1981; Sears 1953). Sears (1953:11) says: "There appears to be a tendency among coelenterates for a seemingly good species to appear in a particular locality, often in considerable numbers, and after a time to disappear, never to be seen again." This must be related to the peculiarity in patchiness and irregular aggregational distribution characteristics of siphonophores and other coelenterate populations, and the ineffectiveness of the plankton sampling gear in capturing these organisms (Biggs, Bidigare, and Smith 1981; Hamner *et al.* 1975). Because of their swimming behavior and speed, and their life cycle characteristics, siphonophores are capable of avoiding capture by plankton nets (Biggs 1977).

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National Marine Fisheries Service, NOAA, Southwest Fisheries Center, P.O. Box 271, La Jolla, California 92038.

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HETEROPYRAMIS ALCALA AND *THALASSOPHYES FERRARII*, NEW SPECIES OF CLAUSOPHYIDAE (CALYCOPHORAE: SIPHONOPHORAE) FROM THE SOUTH PACIFIC

Angeles Alvariño and Kenneth R. Frankwick

Abstract.—Two new species, *Heteropyramis alcala,* and *Thalassophyes ferrarii* are described and compared with the other species of their genera, *Heteropyramis maculata* Moser, 1925, and *Thalassophyes crystallina* Moser, 1925. The material was obtained in the plankton collections made in the South Pacific during the U.S. Antarctic Research Program.

The family *Clausophyidae* Totton and Bargmann, 1965, is characterized by the presence of the somatocyst in both anterior and posterior necotophores. This family includes 5 genera: *Clausophyes,* with two species, *C. ovata* (Kefferstein and Ehlers, 1860), *C. galeata* Lens and van Riemsdijk, 1908; *Chuniphyes,* with two species, *C. multidentata* Lens and van Riemsdijk, 1908; *C. moserae* Totton, 1954; *Crystallophyes* (*C. amigdalina* Moser, 1925); *Heteropyramis* (*H. maculata* Moser, 1925); and *Thalassophyes* (*T. crystallina* Moser, 1925).

The two new Clausophyidae described herein belong to the genera *Heteropyramis* and *Thalassophyes.*

Heteropyramis alcala, new species
Figs. 1–3

Material.—From cruises of R/V *Eltanin* in 1965 and 1966 (see Table 1). Holotype: Polygastric form (nectophore), and eudoxid form (bract + gonophore) from *Eltanin* cruise 25, sta 1697, off Chile, USNM 61064. Paratypes: 1 nectophore, 1 bract, 2 gonophores, from *Eltanin* cruise 16, sta 895, S of New Zealand, USNM 61065.

Etymology.—Named in honor of San Diego de Alcala, patron of the University of San Diego, and the sister city in Spain of San Diego, California.

Description.—Polygastric phase (Fig. 1): The anterior nectophore forms a high pyramid, with a height slightly more than twice its width. It is about 5 mm high and 2.2 mm wide, with 5 ridges. The dorsal and 2 lateral ridges reach the apex of the nectophore, but the 2 ventral ridges only reach a point close to the apex.

The hydroecium is not as deep as in *H. maculata.* It extends up to midlength of the nectophore and is closed by the 2 incomplete ventral ridges which are wider at the inferior part. These ridges have crests of roundish contour at the inferior part.

A series of white triangular spots appear on the lateral ridges and the apex of the nectophore. The ventral ridges and the dorsal ridge have no opaque white spots. In *H. maculata* there are 9 of these spots, one at the apex, another at the

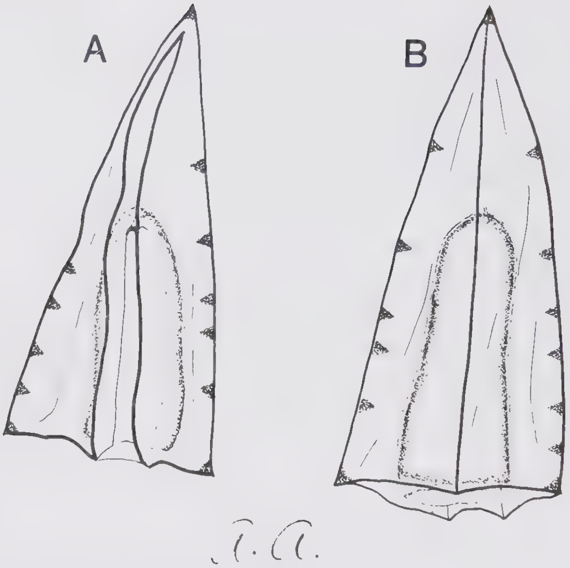

Fig. 1. *Heteropyramis alcala,* nectophore 5 mm high: A, Ventral view; B, Dorsal view.

marginal edge of the lateral ridges, and 2–4 intermediate along those ridges (Totton 1954; Totton and Bargmann 1965).

In *Heteropyramis alcala* the right lateral ridge has 6 opaque white spots, one at the marginal edge, another at midlength of the ridge, 3 about equally spaced between the other 2, and another at midlength of the upper half of the ridge. The left lateral ridge has 7 opaque white spots, one at the marginal inferior corner, another at about midlength of the ridge, and 4 about equally spaced between those 2, plus one at the midpoint of the upper half of the ridge. Another opaque white spot appears at the apex of the nectophore, bringing the total number of opaque white spots to 14.

The nectosac occupies the center of the pyramid, is less than half the width of the nectophore and reaches higher than the midlength of the nectophore. The ostium, opening of the nectosac, is equal in size to the diameter of the nectosac, and the space from the wall of the nectophore to the opening of the nectosac is

Table 1.—Records of *Heteropyramis alcala* in the South Pacific region.

Eltanin cruise	Station	Gear/ tow	Location	Depth	Date	Local time
16	895	MPS[1]	49°17′S, 162°00′E	500–250 m	7 Feb 1965	1110–1124
25	1697	BPS[2]	39°56′S, 85°54′W	1000–500 m	30 Sep 1966	0732–0753
26	1794	BPS	41°58′S, 160°06′E	1000–500 m	7 Dec 1966	1425–1449
26	1803	BPS	47°37′S, 161°49′E	1000–500 m	13 Dec 1966	1052–1112

[1] Multiple plankton sampler.
[2] Bathypelagic plankton sampler.

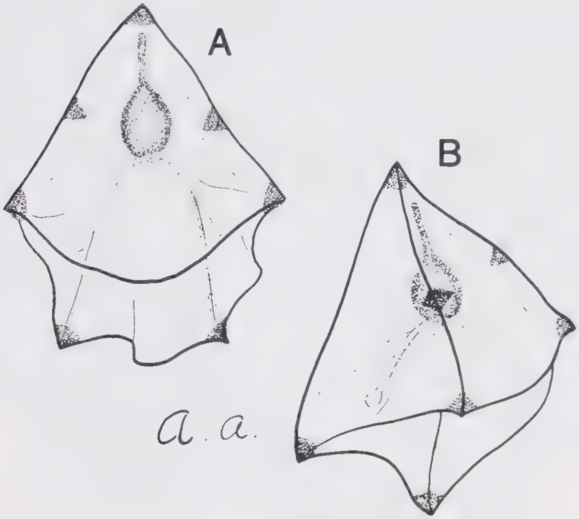

Fig. 2. *Heteropyramis alcala*, bract 3 mm high: A, Dorsal view; B, Left view.

a wide velum. In *H. maculata* the nectosac has a height less than half but more than ⅓ of the nectophore's length.

Eudoxid phase: The bract (Fig. 2) is pyramid-shaped, with 4 triangular sides. It is about 3 mm in height, and 3 mm wide at the base. The ridges of the bract present thin laminar extensions.

White opaque spots in the bract of *Heteropyramis alcala* are distributed as follows: one at the vertex of the bract, one at the base of the ridge of the pyramid, and one at the midlength of each of the 2 ridges which form the dorsal side of the bract. This distribution of the white spots differs from that of *Heteropyramis*

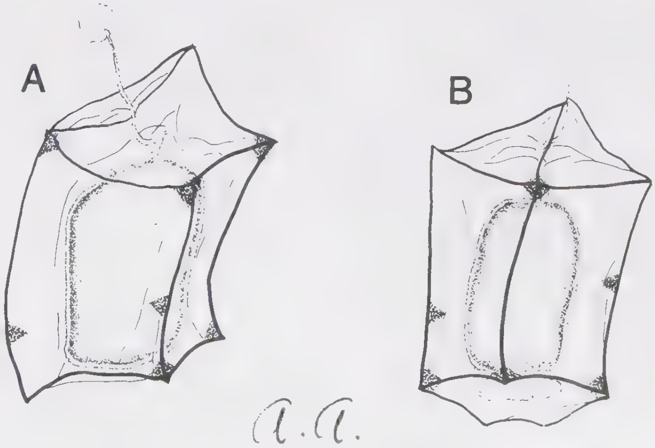

Fig. 3. *Heteropyramis alcala*, gonophore 2.5 mm high: A, Lateral view; B, Dorsal view.

maculata, which displays one apical white spot and one spot at the base of each dorsolateral ridge.

The phylocyst of *Heteropyramis alcala* is in form of a little bottle, quite different from the shape of that of *H. maculata.*

The hydroecial canals are shorter than those of *H. maculata.*

The gonophore (Fig. 3) is pentagonal-prismatic in shape, has 5 ridges, and the top forms a short pyramid. One ridge has opaque white spots at the inferior margin and the upper margin, and the other has 3 equidistant spots along the ridge, from the inferior to the upper margins. Another ridge has one spot at the inferior margin and at midlength of the ridge, and the fourth ridge has one spot at the upper corner and one at the inferior part, at about ¼ of the distance to the inferior margin. The fifth ridge has no opaque white spots.

The closely related species *H. maculata* Moser, 1925 is found mainly in the tropical oceanic regions (Alvariño 1971), and was obtained by Leloup and Hentschel (1938) west of South Georgia Islands.

Thalassophyes ferrarii, new species
Figs. 4–5

Material.—From cruises of R/V *Eltanin* in 1966 (see Table 2). Holotype: 1 superior nectophore and 1 inferior nectophore from *Eltanin* cruise 25, sta 1710, off Chile, USNM 61066. Paratype: 1 superior nectophore and 4 inferior nectophores from *Eltanin* cruise 26, sta 1794, Tasman Sea, USNM 61067.

Table 2.—Records of *Thalassophyes ferrarii* in the South Pacific region.

Eltanin cruise	Station	Gear/ tow	Location	Depth of haul	Date	Local time
25	1710	BPS	42°11′S, 86°03′W	2000–1000 m	5 Oct 1966	2020–2051
26	1794	BPS	41°58′S, 160°06′E	1000–500 m	7 Dec 1966	1425–1449
26	1803	BPS	47°37′S, 161°49′E	1000–500 m	13 Dec 1966	1052–1112

Etymology.—Named for Dr. Frank Ferrari in appreciation of his dedication and encouragement in behalf of plankton studies and his valuable assistance in developing this research.

Description.—Polygastric phase: The superior nectophore (Fig. 4) is about 7 mm high and 2 mm wide, or less than half as wide as its height. It has 5 ridges, all reaching to the apex of the nectophore, and each displaying crests. The crest of the dorsal ridge is the narrowest, and the crests of the ventral ridges the widest; widest at about the posterior third of the nectophore, forming a roundish contour of serrate edges. The lateral ridges have wide crests at the low part of the ridge, close to the ostium, ending at that region in a round edge.

The hydroecium is shallow, reaching less than half the height of the nectophore.

The long narrow nectosac reaches near the top of the nectophore. The space at the lowest part of the nectophore, between the wall of the nectophore and the opening of the nectosac is closed by the velum, which is wide.

In *Thalassophyes crystallina* Moser, 1925, the hydroecium is deep and extends up to more than half the height of the nectophore. The ridges with crests are quite different in *T. crystallina* and *T. ferrarii.* In the former, the crests are narrow or

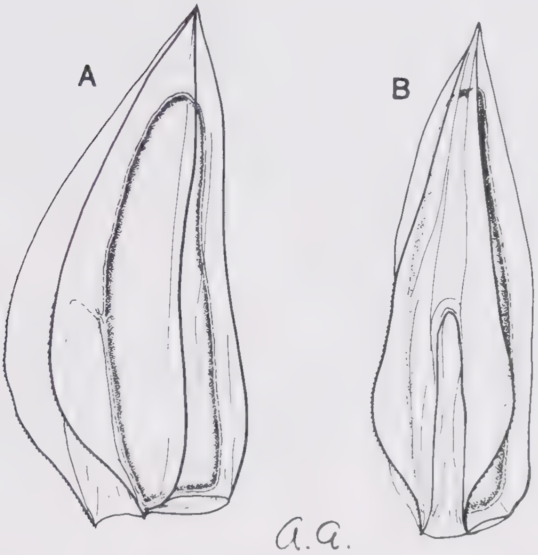

Fig. 4. *Thalassophyes ferrarii,* superior nectophore 7 mm long: A, Lateral view; B, Ventral view.

absent; in the latter they are wide and roundish at the lowest part, presenting serrate edges along the crests of the ventral ridges. The nectosac in *T. crystallina* reaches up to half the height of the nectophore, whereas in *T. ferrarii* it nearly reaches the apex of the nectophore.

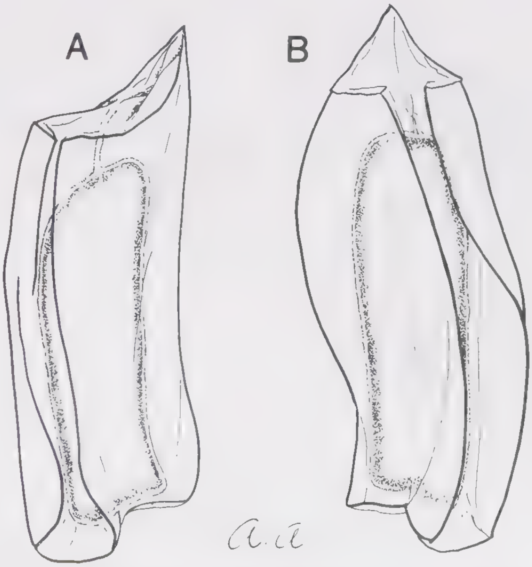

Fig. 5. *Thalassophyes ferrarii,* inferior nectophore 6 mm long: A, Lateral view; B, Ventral view.

The inferior nectophore (Fig. 5) is prismatic with an apical triangular prolongation at the dorsal side. The dorsal ridge has no crest. The lateral ridges develop a wing-like crest at the upper part, diminishing toward the low region, to end with no crest at the ostium level. The ventral ridges are pleated at the top, like two doors or flaps, forming the hydroecial folds, and covering the hydroecial tunnel-like cavity; at the low part, the ridges with crests are united by a round flap extending down from the region of the ostium.

Eudoxid phase: None observed.

The closely related species *T. crystallina* is found mainly in the Antarctic and adjacent regions (Alvariño 1971).

The scarcity and erratic distribution of most of the species of Siphonophorae, Medusae and Chondrophorae is not strange to scholars working on these groups. This peculiar phenomenon, pointed out by Alvariño (1971, 1981), Biggs (1977), Biggs, Bidigare and Smith (1981), and Sears (1953) is due to the particular behavior of these coelenterates. The resulting scattered aggregations of populations, the speed and swimming characteristics enable these animals to avoid capture by plankton nets.

Acknowledgments

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(AA) National Marine Fisheries Service, NOAA, Southwest Fisheries Center, P.O. Box 271, La Jolla, California 92038; (KRF) University of San Diego, Alcala Park, San Diego, California 92110.

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DESCRIPTION OF THE LARVAE OF THE CUSK EELS *OPHIDION SCRIPPSAE* AND *CHILARA TAYLORI* (FAMILY OPHIDIIDAE)

DAVID A. AMBROSE, JOHN L. BUTLER, H. GEOFFREY MOSER,
BARBARA Y. SUMIDA, ELAINE M. SANDKNOP, AND ELIZABETH G. STEVENS
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038

ABSTRACT

Larvae of the two species of cusk eels (Ophidiidae) found in the CalCOFI region, *Ophidion scrippsae* and *Chilara taylori*, are described from specimens reared in the laboratory and from specimens collected in the field. Larvae are distinguished by morphological, meristic, and pigment-pattern differences. *C. taylori* larvae are proportionately longer and more slender, have more vertebrae, and have more dorsal and anal fin rays than do *O. scrippsae*. The gut loop forms at a longer body length in *C. taylori* (ca. 14.1 mm) than in *O. scrippsae* (ca. 7.5 mm). *O. scrippsae* larvae have no pigment in the caudal fin, and the anal fin usually has numerous melanophores, whereas *C. taylori* larvae have caudal fin pigment and little, if any, pigment in the dorsal and anal fins. Analysis of ophidiid larvae collected in CalCOFI survey cruises from 1972 to 1978 revealed a relatively low abundance and a distribution centered around points and capes from San Diego to the vicinity of Magdalena Bay, reflecting the nearshore nature of these fish.

RESUMEN

Se describen las larvas de dos especies de Ophidiidae, *Ophidion scrippsae* y *Chilara taylori*, obtenidas en la región explorada por el programa CalCOFI. Los ejemplares estudiados proceden de cultivos en el laboratorio y material recolectado en el mar. Las larvas de estas dos especies se distinguen por las características morfológicas, merísticas y la distribución del pigmento. Las larvas de *C. taylori* son más largas y delgadas, tienen más vertebras y más radios en las aletas dorsal y anal, que las larvas de *O. scrippsae*. En *C. taylori*, el asa del tubo digestivo se forma cuando los ejemplares alcanzan unos 14.1 mm, mientras que en *O. scrippsae* ya aparece en larvas de 7.5 mm de longitud. Las larvas de *O. scrippsae* carecen de pigmento en la aleta caudal, pero en la aleta anal aparecen generalmente muchos melanoforos. En *C. taylori* las larvas presentan la aleta caudal pigmentada y escaso o ningún pigmento en las aletas dorsal y anal. Los Ophididos recolectados desde San Diego hasta las cercanías de Bahía Magdalena, durante los cruceros CalCOFI, en el periodo 1972-1978, no han sido abundantes, y aparecen concentrados en las zonas de cabos y salientes de la costa, lo que indica que estos peces son de régimen nerítico.

INTRODUCTION

Two species of cusk eels (Ophidiidae) are found in the CalCOFI region, *Ophidion scrippsae* and *Chilara taylori* (Robins et al. 1980). *O. scrippsae* ranges from the Gulf of California north of Guaymas, Mexico, to Point Arguello, California, (ca. 34°N) in depths of 3 m to 76 m. *C. taylori* has been taken from San Cristobal Bay, Baja California, (ca. 27°N) to northern Oregon from depths of 1 m to over 260 m (Miller and Lea 1972).

Neither species is fished commercially, but both are often taken with bottom trawling gear, purse seines, and bait nets. Cusk eels are preyed upon by numerous commercially important fishes, diving sea birds, and California sea lions (Fitch and Lavenberg 1968). Primarily nocturnal, adult cusk eels are burrowing tail-standers inhabiting a variety of substrates including silty sand and green mud (Mearns 1979), eel grass (Herald 1953), rubble, crevices, and holes (Fitch and Lavenberg 1968). The pelagic larvae are collected in coastal CalCOFI plankton tows primarily in the fall.

The purpose of this paper is to describe the development of the early larval stages of *O. scrippsae* and *C. taylori* and to summarize the distribution of larvae in CalCOFI samples made from 1972-78.

METHODS AND MATERIALS

Life-history series for *O. scrippsae* were assembled from larvae reared at the Southwest Fisheries Center from eggs collected in plankton tows at La Jolla Cove. Some early larval stages of *C. taylori* were obtained by rearing batches of mixed, unidentified eggs collected in nearshore plankton tows; however, most of the specimens were obtained from CalCOFI plankton tows. Reared fish were kept at 17.6°-20.6°C in black 100-liter pots and fed *Brachyonis* (a rotifer), harpacti-

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coid copepods, and *Artemia* (a brine shrimp). We attempted to maintain the prey concentrations at approximately 50 *Brachyonis*/ml, and the copepods and *Artemia* both at 1/ml.

A series was established for the study of morphological development, morphometry, and pigment formation using the techniques and terminology of Ahlstrom et al. (1976). Another series was stained in Alizarin Red-S and X-rayed to obtain meristic data.

DESCRIPTION

Literature

Larvae of two Atlantic species of *Ophidion* have been described: *O. vassali* (Padoa 1956) and *O. barbatum* (Padoa 1956; Aboussouan 1972).

Distinguishing Features

O. scrippsae eggs are slightly off-round, and have homogenous yolk, no oil globule, and a mean size of 1.00 × 1.06 mm. Larvae are 2.5 mm long at hatching, are slender, and have a gut that ends just short of mid-body. The eggs of *C. taylori* are unknown.

Larvae of *O. scrippsae* and *C. taylori* may be distinguished from those of the bythidid *Brosmophysis marginata* on the basis of myomere count and pigmentation. *B. marginata* have 63-65 vertebrae compared with 67-69 for *O. scrippsae* and 86-91 for *C. taylori*. *B. marginata* larvae lack pigment at the finfold margin and have five large blotches along the dorsum, four postanal and ventral blotches, and a diffuse band near the tip of the notochord.

The larval morphology, meristics, and pigmentation patterns of *O. scrippsae* and *C. taylori* are unique to these species. *C. taylori* larvae are proportionately longer and more slender than *O. scrippsae*. Notochord flexion occurs at a much larger size in *C. taylori* larvae (21.1-29.6 mm) than in *O. scrippsae* (9.6-11.5 mm). The gut loop forms at a longer body length in *C. taylori* (ca. 14.1 mm) than in *O. scrippsae* (ca. 7.5 mm). *O. scrippsae* has fewer dorsal fin rays (136-153) and anal fin rays (112-119) than does *C. taylori* (198-216 dorsal and 156-170 anal fin rays). *O. scrippsae* larvae have no pigment in the caudal fin, and the anal fin usually has numerous melanophores, whereas *C. taylori* larvae have caudal fin pigment and little, if any, pigment in the dorsal or anal fins.

Ophidion scrippsae

Morphology. Ophidion scrippsae eggs are slightly off-round with a mean size of 1.00 × 1.06 mm. They possess a homogenous yolk, a wide perivitelline space, and no oil globule. The elongate slender larvae (body depth only 10% of body length) hatch at about 2.5 mm in a relatively undifferentiated state, with eyes incompletely formed and unpigmented. The larvae have a straight tubular gut, a large yolk-sac, and no mouth, branchial apparatus, or pectoral fins. By 3.8 mm (3 days after hatching) the yolk-sac has been absorbed, the eyes are pigmented, and the mouth and pectoral fins have formed (Figure 1). Notochord flexion occurs between 9.6-11.5 mm body length (Table 1). Morphological proportions are summarized in Table 2. Ontogenetic trends show a relative shortening of the gut length, a decrease in the relative eye size, an increase in body depth, and the anterior migration of the pelvic fins.

Timing, positioning, and size at torsion of the gut in ophidiid larvae are useful taxonomic characters (D. J. Gordon, Univ. of Miami, pers. comm.). The gut of *O. scrippsae* coils at a size range of 7.5-8.5 mm on about the 18th day after hatching (Figure 2). Coiling is always in the same direction, with the posterior portion of the gut displaced away from the observer when the left side of the larva is viewed. The single coil occupies a large middle portion of the visceral cavity.

Fin formation and meristics. Dorsal and anal fin pterigiophores begin to ossify by the onset of notochord flexion at about 9.6 mm (Table 3). The full complement of anal fin rays (112-119) and dorsal fin rays (136-153) are ossified near the end of notochord flexion. Pelvic fin buds are visible at the start of notochord flexion, and as growth proceeds one ray of each pair becomes longer. Pectoral fin and principal caudal fin rays begin ossification near the end of the notochord flexion period at ca. 11.5 mm body length. Ossification of the vertebral column begins after notochord flexion. By ca. 15.8 mm, the pectoral and caudal fins attain their full complement of rays (22-24 and 4 + 5, respectively), and the full complement of 67-69 vertebrae is ossifying.

Pigmentation. O. scrippsae larvae are unpigmented at hatching. By the second day (2.8-3.0 mm) small melanophores are forming over the entire body, giving the larvae a speckled appearance. At day 4 (3.6-3.9 mm) serial melanophores are present near the margins of the dorsal and anal fin folds, and along the dorsal and ventral margins of the body (Figure 1). Melanophores are sparse or lacking laterally on the body, and the eyes are becoming pigmented. After gut torsion on about the 18th day (ca. 7.5 mm), little pigment remains in the dorsal fin fold. Melanophores on the anal fin fold and developing anal fin increase in density, and pigment begins to appear over the branchiostegal rays. Body pigment is still primarily at the dorsal and ventral margins, but is becoming more diffuse. By the 45th day (ca. 20.3 mm, Figure 3) a few scattered melanophores appear on top of the brain, and

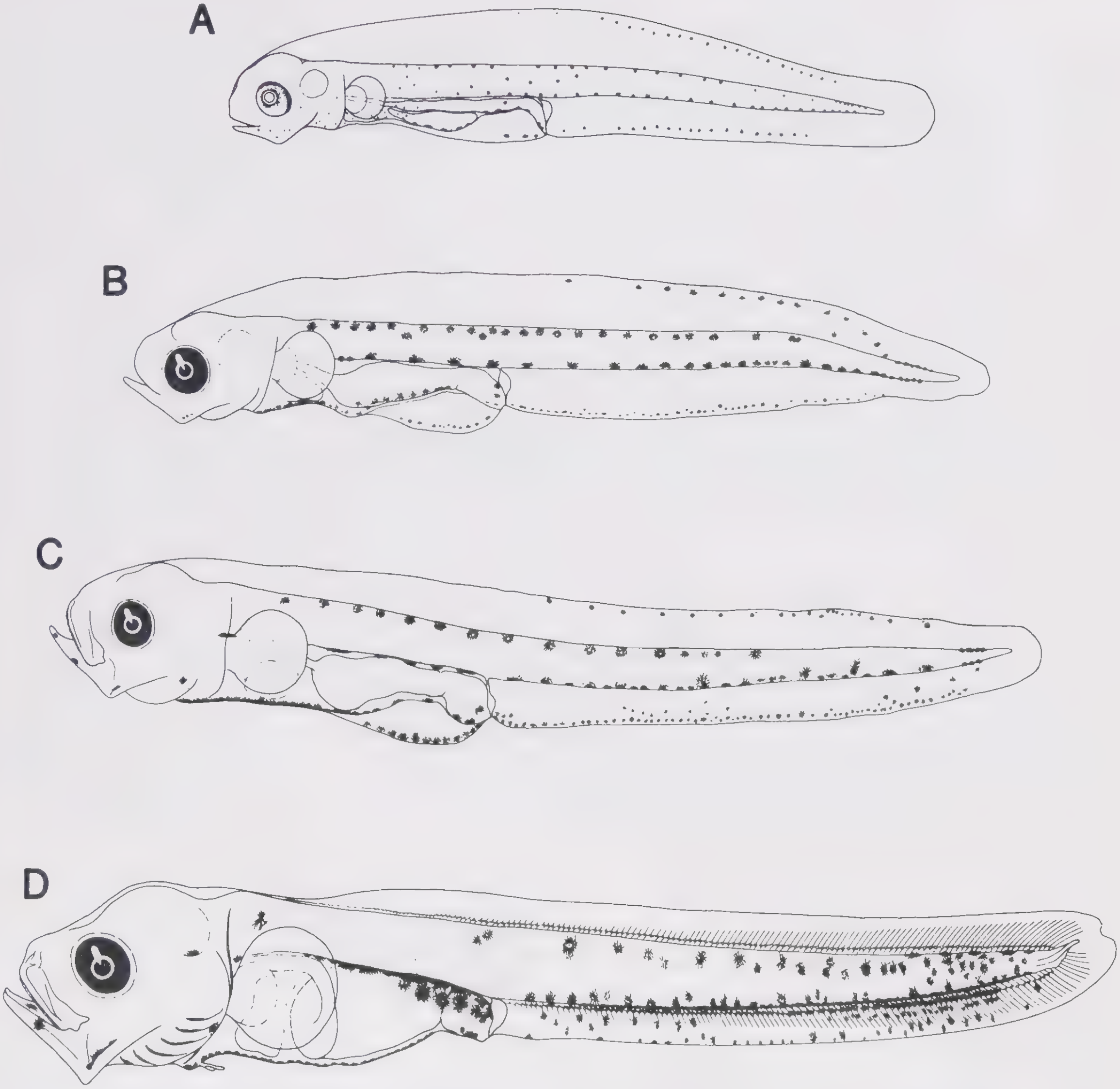

Figure 1. Larvae of *Ophidion scrippsae:* (*A*) 3.8 mm with yolk remnant, day 4; (*B*) 4.8 mm, day 8; (C) 7.1 mm, day 14; (*D*) 10.6 mm, day 42.

the ventral surface of the gut becomes less pigmented. The caudal fin remains unpigmented throughout the larval development of *O. scrippsae*.

Xanthophores are conspicuous along the dorsal and ventral body margins and in the dorsal fin fold in living *O. scrippsae* larvae. This pigment fades rapidly after fixation, leaving only the melanophores. By 14.7 mm, the xanthophores highlight the dorsal body surface, and melanophores dominate the anal fin and ventral body, producing a complementary effect similar to that discussed by Moser (1981).

Behavior. O. scrippsae larvae were active water-column feeders, especially around the edges of the tank, until about 36 days after hatching, when they settled to the bottom and lay in wait for their prey. By day 41, many of the larvae had burrowed into the sand at the bottom of the tank, in a manner similar to adult behavior.

TABLE 1
Measurements in mm of Reared Developmental Series of *Ophidion scrippsae*

Age days	Body length	Snout to anus	Head length	Snout length	Eye diameter	Body depth at pectoral fin base	Snout to dorsal fin origin	Snout to anal fin origin	Snout to pelvic fin origin	Pectoral fin length	Pelvic fin length long	Pelvic fin length short	
2	3.2	1.7	.64	.16	.06	.16	—	—	—	—	—	—	yolk-sac
4	3.8	1.8	.60	.12	.22	.36	—	—	—	.12	—	—	yolk-sac
5	4.0	1.8	.62	.16	.22	.42	—	—	—	.16	—	—	
8	4.8	2.1	.76	.18	.26	.44	—	—	—	.24	—	—	
8	5.4	2.5	.86	.26	.26	.54	—	—	—	.20	—	—	
10	6.1	2.8	1.1	.23	.32	.70	—	—	—	.20	—	—	
12	6.7	3.0	1.1	.30	.34	.68	—	—	—	.40	—	—	
14	7.1	3.2	1.2	.40	.32	.86	—	—	—	.40	—	—	
19	7.2	3.2	1.2	.34	.38	.90	—	—	—	.46	—	—	
21	7.5	3.3	1.3	.36	.40	1.0	—	—	—	.60	—	—	
21	7.8	3.3	1.4	.36	.40	1.0	—	—	—	.56	—	—	
16	8.2	3.7	1.3	.44	.38	1.0	—	—	.72	.50	—	—	
24	9.6	4.6	2.2	.72	.48	1.6	3.3	4.6	1.8	.60	—	—	
24	10.0	4.6	1.9	.56	.48	1.7	3.3	4.6	1.9	.60	—	—	
42	10.6	4.9	2.2	.67	.58	1.7	3.3	5.1	1.8	.80	.24	.14	
31	11.0	4.9	2.2	.58	.67	1.8	3.1	5.1	1.9	.80	.26	.14	
36	11.5	5.4	2.4	.76	.67	1.8	3.8	5.4	2.0	1.0	.20	.16	
36	13.2	5.6	2.6	.67	.68	2.2	3.6	5.7	2.3	1.2	.34	.28	
44	15.0	6.2	2.7	.83	.67	2.5	3.8	6.3	2.0	1.1	—	—	
55	15.8	6.3	2.9	.75	.80	2.5	3.9	6.6	2.1	1.0	.72	.56	
55	17.2	6.8	3.2	.90	.83	2.4	4.8	6.8	2.3	1.0	.70	.50	
50	19.6	8.3	3.7	.92	.92	3.2	5.2	7.8	2.1	1.2	1.1	.60	
38	20.3	8.0	3.3	.75	.92	3.3	4.7	7.9	2.1	1.6	.90	.60	
55	21.3	7.8	4.0	1.0	.92	3.1	5.2	8.0	2.1	1.8	1.1	.70	
45	21.7	8.5	4.3	.92	.92	2.8	5.5	8.5	1.8	1.4	1.2	.80	
50	21.9	8.4	4.1	1.0	.93	3.2	5.5	8.5	2.0	1.8	1.2	.80	
43	22.3	8.1	4.1	1.0	.92	2.8	5.0	8.1	2.2	2.0	1.3	.82	
49	22.7	8.7	4.4	1.1	1.0	3.2	6.0	8.7	2.5	2.0	1.6	1.0	
43	23.2	8.7	4.1	1.0	.92	3.2	5.8	9.0	2.6	1.6	1.4	.84	
50	23.2	9.6	4.2	1.0	1.1	3.8	6.5	9.7	1.5	2.0	1.2	.70	
55	24.7	9.3	4.6	1.2	1.0	3.5	6.0	9.2	2.2	2.4	1.6	.80	
50	25.2	9.6	4.6	1.1	1.1	3.8	6.3	9.5	2.1	1.9	1.9	1.0	
50	27.4	11.0	5.4	1.3	1.3	4.3	7.2	11.2	2.0	2.8	2.2	1.2	

Specimens between dashed lines are undergoing notochord flexion.

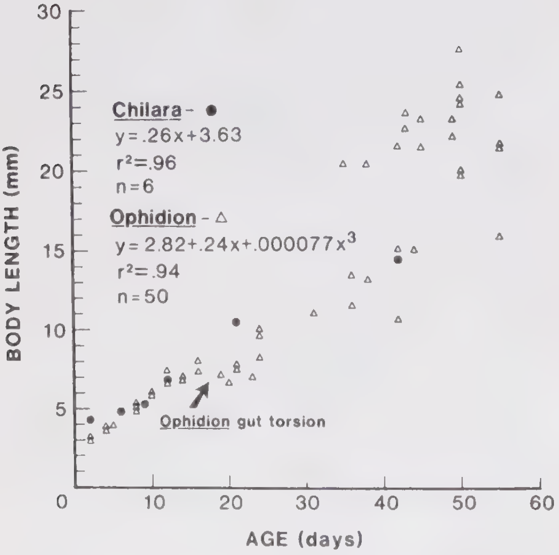

Figure 2. Growth rates of reared *Ophidion scrippsae* and *Chilara taylori*.

Chilara taylori

Morphology. *C taylori* larvae are relatively larger at hatching and at subsequent developmental stages compared with *O. scrippsae* larvae, but follow similar developmental trends such as the anterior migration of the pelvic fins and the relative shortening of the gut length. The gut of *C. taylori* begins to loop at ca. 13.3 mm. Looping is in the same direction as in *O. scrippsae*, but the coil is relatively smaller and is usually located slightly more posteriad in the visceral cavity. Notochord flexion occurs at ca. 20-30 mm body length (Table 4). Morphologial proportions are summarized in Table 2.

Fin formation and meristics. Dorsal and anal fin pterigiophores begin to ossify before notochord flexion at ca. 15.1 mm. Full anal fin (156-170) and dorsal fin (198-216) ray complements are ossifying near the end of notochord flexion at 29.6 mm (Table 3). Pelvic fin buds become visible at the start of flexion, and one ray is longer than the other in each pair by ca. 29.0 mm. Pectoral fin and principal caudal fin rays

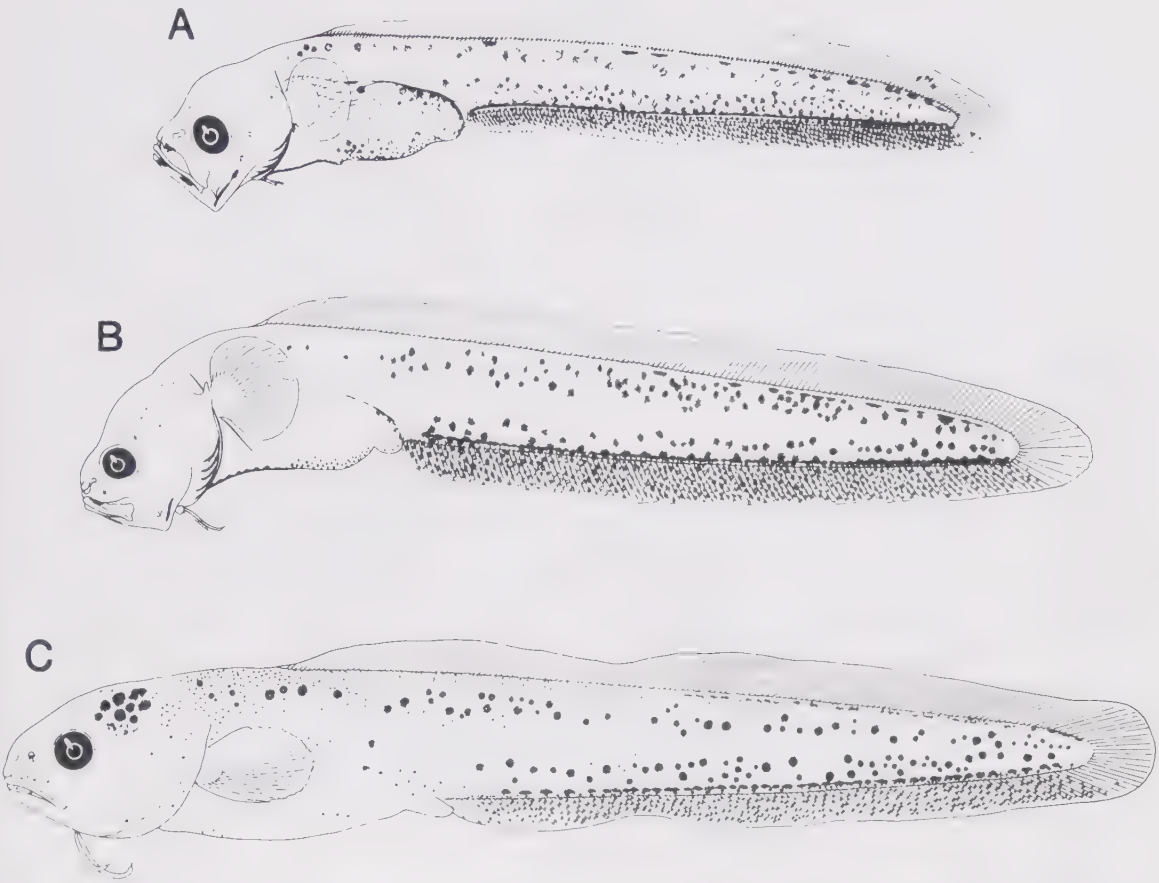

Figure 3. Developmental stages of *Ophidion scrippsae:* (*A*) 15.0-mm larva, day 44; (*B*) 20.3-mm larva, day 35; (*C*) 27.4-mm juvenile, day 50.

TABLE 2

Body Proportions of Larvae of *Ophidion scrippsae* and *Chilara taylori*

Body proportion	N	Snout to anus / body length	Head length / body length	Snout length / head length	Eye diameter / head length	Body depth at pectoral fin base / body length	Snout to dorsal fin / body length	Snout to anal fin / body length	Snout to pelvic fin / body length	Pectoral fin height / body length
Ophidion scrippsae										
Preflexion	12	45.5 ± 2.68 (42-53)	16.9 ± 1.24 (16-20)	26.8 ± 4.22 (20-34)	29.4 ± 7.04 (9-37)	10.7 ± 2.31 (5-13)	—	—	8.9 N = 1	5.3 ± 1.62 N = 11 (3-8)
Flexion	5	46.4 ± 1.14 (45-48)	20.8 ± 1.48 (19-23)	30.0 ± 2.74 (26-33)	26.2 ± 3.03 (22-30)	16.4 ± 0.55 (16-17)	31.8 ± 2.39 (28-34)	47.0 ± 1.00 (46-48)	17.8 ± 1.10 (17-19)	7.2 ± 1.30 (6-9)
Postflexion	16	39.2 ± 1.76 (36-42)	18.6 ± 1.02 (16-20)	24.9 ± 2.21 (21-31)	24.3 ± 2.14 (21-28)	15.1 ± 1.29 (13-17)	25.3 ± 1.66 (22-28)	39.6 ± 2.00 (36-43)	10.4 ± 2.73 (6-17)	7.9 ± 1.41 (6-10)
Chilara taylori										
Preflexion	24	38.7 ± 3.25 (31-44)	12.5 ± 1.69 (8-15)	25.1 ± 4.48 (14-31)	31.5 ± 5.58 (23-41)	8.2 ± .97 (7-9) N = 22	26.5 N = 1	35.9 N = 1	12.9 N = 1	3.4 ± .91 (2-5) N = 22
Flexion	3	30.7 ± 1.53 (29-32)	11.7 ± 1.15 (11-13)	28.7 ± 2.52 (26-31)	23.7 ± 2.08 (22-26)	7.3 ± .58 (7-8)	18.0 ± 3.61 (15-22)	31.0 ± 3.00 (28-34)	10.0 ± 2.00 (8-12)	2.7 ± .58 (2-3)
Postflexion	3	27.3 ± 2.08 (25-29)	12.3 ± 1.53 (11-14)	24.7 ± 3.21 (21-27)	23.3 ± 2.89 (20-25)	7.3 ± .58 (7-8)	17.0 ± 0 (17)	27.7 ± 1.53 (26-29)	7.3 ± .58 (7-8)	2.7 ± .58 (2-3)

Values are expressed as percentage of body or head length (mean, standard deviation, and range).

TABLE 3
Meristics of Larvae of *Ophidion scrippsae* and *Chilara taylori*

Size (mm)	Dorsal fin	Anal fin	Pectoral fin	Caudal fin	Vertebrae	Branchiostegal rays	Gill rakers
Ophidion scrippsae							
4.0	—	—	—	—	—	—	—
6.1	—	—	—	—	—	—	—
7.8	—	—	—	—	—	4	—
9.6	104	96	—	—	—	7	—
11.5	138	118	5	2 + 5	—	7	0 + 5
15.8	139	113	24	4 + 5	67	7	0 + 5
19.6	146	116	22	4 + 5	67	7	3 + 5
21.9	148	117	22	4 + 5	67	7	2 + 6
24.7	141	112	22	4 + 5	67	7	3 + 7
Adult complement	136-153	112-119	22-25	4 + 5	67-69	7	—
Chilara taylori							
4.6	—	—	—	—	—	—	—
7.6	—	—	—	—	—	—	—
10.4	—	—	—	—	—	—	—
14.1	—	—	—	—	—	6	—
21.1	180	163	6	3 + 5	—	7	0 + 7
29.6	203	168	22	4 + 5	—	7	0 + 8
32.6	203	162	22	4 + 5	—	7	0 + 8
36.1	210	168	22	4 + 5	91	7	0 + 7
47.0	204	163	25	4 + 5	90	7	3 + 8
Adult complement	198-216	156-170	22-25	4 + 5	86-91	7	1-4 + 5-9

Specimens between dashed lines are undergoing notochord flexion.

TABLE 4
Measurements in mm of Developmental Series of *Chilara taylori*

Station or age (day)	Body length	Snout to anus	Head length	Snout length	Eye diameter	Body depth at pectoral fin base	Snout to dorsal fin origin	Snout to anal fin origin	Snout to pelvic fin origin	Pectoral fin length	Pelvic fin length	
											long	short
5910- 80.52	3.6	1.1	.28	.04	.08	.32	—	—	—	—	—	—
7510- 97.50	3.9	1.6	.44	.12	.18	.24	—		—	—	—	—
6310- 80.51	4.3	1.7	.60	.12	.22	.38	—	—	—	.14	—	—
2	4.3	1.9	.63	.12	.24	.38	—	—	—	.12	—	—
6706-120.35	4.6	1.8	.60	.10	.20	.44	—	—	—	.12	—	—
6	4.8	2.0	.72	.16	.24	.41	—	—	—	.20	—	—
4	5.0	2.2	.68	.13	.24	.38	—	—	–	.20	—	—
9	5.2	2.2	.68	.16	.28	.40	—	—	—	.24	—	—
6706-120.35	5.6	2.3	.64	.16	.24	.60	—	—	—	.24	—	—
Bathtub Rock	6.7	2.7	.72	.17	.26	.52	—	—	–	.26	—	—
12	7.3	2.8	.90	.28	.30	.48	—	—	—	.40	—	—
6706-120.35	7.6	3.1	.76	.20	.28	.60	—	—	—	.28	—	—
6310- 80.51	8.2	3.3	.96	.24	.28	.64	—	—	—	.20	—	—
6310- 80.51	9.7	3.6	1.00	.28	.32	.68	—	—	—	.28	—	—
21	10.4	3.9	1.30	.37	.40	.76	—	—	—	.48	—	—
5711- 87.36	10.5	4.2	1.40	.40	.36	.80	—	—	—	.32	—	—
7207-117.40	10.6	3.7	1.28	.40	.37	1.00	—	—	—	.40	—	—
5910- 80.52	12.1	4.8	1.72	.68	.40	.96	—	—	—	.34	—	—
6107-93.55	12.6	4.6	1.48	.40	.36	.88	—	—	—	.34	—	—
6310- 80.51	13.3	5.0	1.80	.44	.42	1.00	—	—	—	.34	—	—
6609-113.65	14.1	5.0	2.00	.58	.50	1.17	—	—	—	.36	—	—
42	14.4	5.5	2.00	.58	.60	1.20	—	—	—	.48	—	—
6210- 77.55	15.0	5.0	2.00	.56	.48	1.16	—	—	—	.36	—	—
6110- 83.55	15.1	5.3	2.00	.56	.52	1.24	4.00	5.42	1.96	.28	—	—
6706-113.35	21.1	6.7	2.67	.83	.58	1.50	4.60	7.08	2.48	.53	.20	—
6210- 80.60	22.5	7.0	2.58	.76	.60	1.56	3.80	7.08	2.20	.52	—	—
6110- 83.70	29.6	8.6	3.25	.83	.83	2.25	4.50	8.33	2.50	.88	.28	.14
5206-107.55	32.6	9.3	3.75	1.00	.92	2.50	5.67	9.42	2.33	1.00	.44	.24
6908- 73.60	36.1	10.0	4.00	.83	1.00	2.67	6.17	10.00	3.00	.88	.68	.52
6110- 63.60	47.0	11.8	6.50	1.69	1.33	3.33	8.00	12.17	3.08	1.24	1.48	1.04

Specimens between dashed lines are undergoing notochord flexion

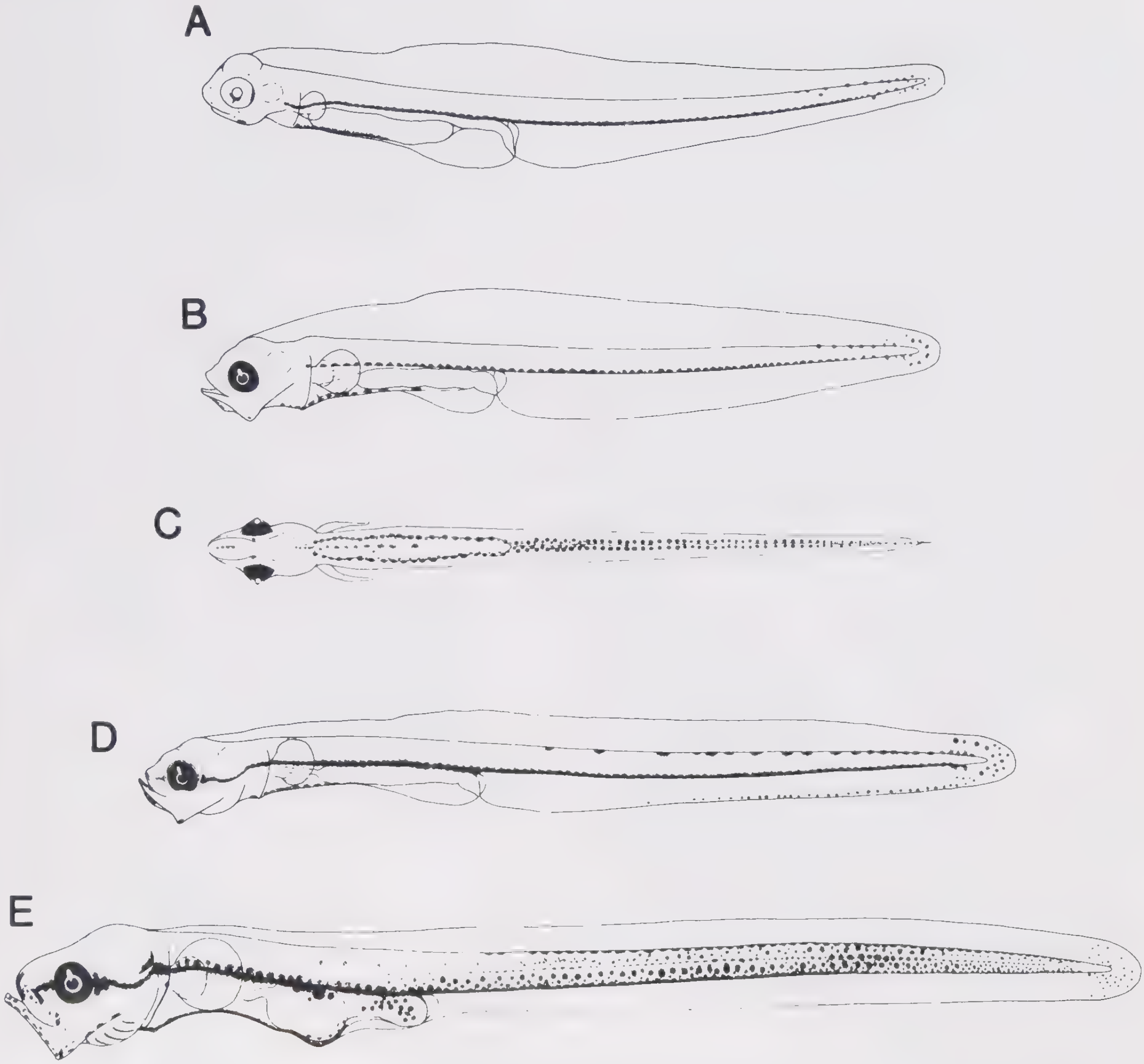

Figure 4. Larvae of *Chilara taylori*: (*A*) 5.0 mm with yolk remnant, day 4; (*B*) 4.8 mm, day 6; (*C*) 4.8 mm, day 6; (*D*) 7.3 mm, day 12; (*E*) 14.4 mm, day 42.

begin to ossify early during the notochord flexion period at ca. 21.1 mm. The adult complement of 4 + 5 principal caudal rays is formed near the end of notochord flexion at ca. 29.6 mm. Ossification of the vertebral column begins after the completion of notochord flexion, and the full complement of 86-91 vertebrae is ossified by 36.1 mm.

Pigmentation. Yolk-sac *C. taylori* larvae have unpigmented eyes and melanophores along the ventral region of the body (Figure 4). By the 6th day after hatching the eyes are pigmented; the yolk-sac has been absorbed; stellate melanophores are frequently present in the caudal fin fold; and two serial rows of ventral melanophores become quite conspicuous. Pigment appears in the angular region of the jaw at about this time and persists throughout larval development. By ca. 6.0 mm, the ventral body pigment line extends anteriorly along the base of the brain and onto the snout. This head pigment persists until at least 15.0 mm but is usually lost by 21.0 mm. By 10.6 mm, the lateral midline becomes pigmented in the caudal region, and the ventral body melanophores increase in number. By 14.4 mm, the caudal region is highly pigmented, and the characteristic lateral midline stripe is heavier. Ventral body pigment decreases and becomes more scattered by 36.1 mm. The dorsal fin fold remains unpigmented throughout larval development, whereas the characteristic caudal fin pigment persists from as early as 4.8 mm. Xanthophores highlight the dorsal and ventral body surfaces of living *C. taylori* larvae.

DISTRIBUTION

Ophidiid larvae occur in comparatively low numbers in CalCOFI samples; however, this probably reflects the relatively low sampling effort in the nearshore region inhabited by these fish. *O. scrippsae* occurred in only 24 (1%) and *C. taylori* in 16 (0.7%) of the 2,361 tows made seaward to station 50 on all CalCOFI lines occupied during 1972-78 (Figure 5). Forty-five *O. scrippsae* larvae were collected in these tows: 4% were captured in June, 7% in August, and 89% in October. Distribution centered around points and capes from San Diego to the vicinity of Magdalena Bay, and around the inshore areas of Viscaino Bay and San Cristobal Bay.

During the same period, 22 *C. taylori* larvae were collected: 4% were taken in February, 4% in July, 28% in August, and 60% in October. Distribution centered around Punta Eugenia at Viscaino Bay, but larvae were collected as far north as Cape Flattery, Washington, and south to San Cristobal Bay. *C. taylori* larvae were collected farther offshore than the majority of the *O. scrippsae* larvae; however, the larval size of both species appeared to be independent of the distance offshore.

The CalCOFI stations at which larval cusk eels were captured tended to be in areas where the adult habitat extended farther offshore either at points of land or in the vicinity of bays where the shelves are broader.

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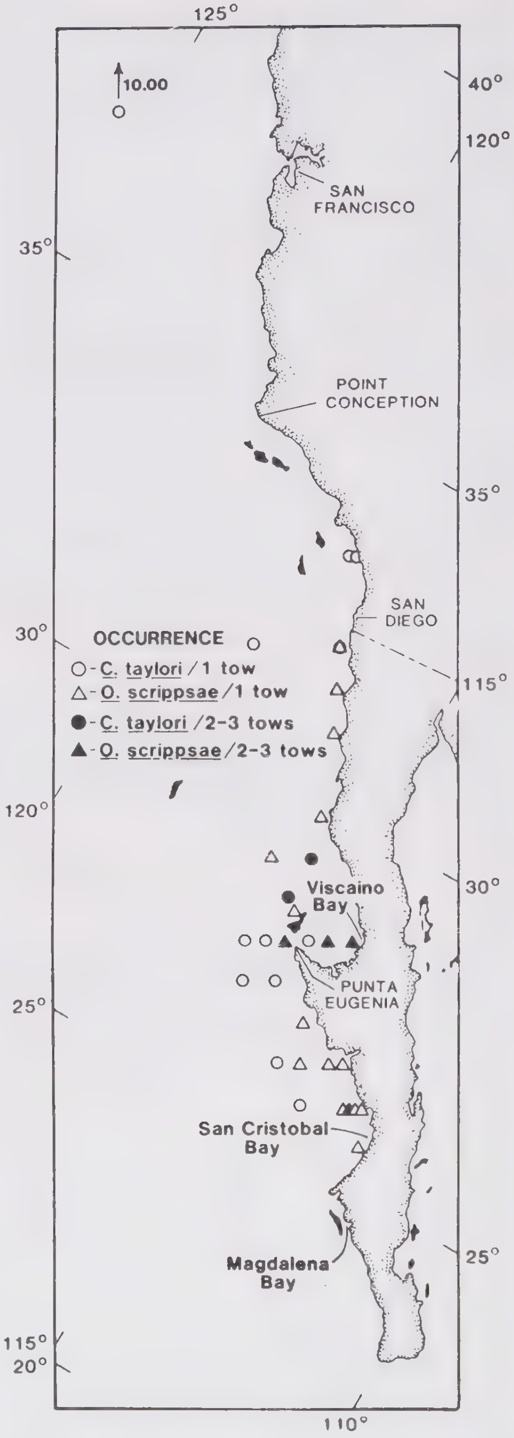

Figure 5. Distribution of *Chilara taylori* and *Ophidion scrippsae* larvae in CalCOFI tows made during 1972-78.

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8308

THE VISUAL FEEDING THRESHOLD AND ACTION SPECTRUM OF NORTHERN ANCHOVY (*ENGRAULIS MORDAX*) LARVAE

TEODORA BAGARINAO[1] AND JOHN R. HUNTER
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038

ABSTRACT

The visual feeding threshold and action spectrum of 10-15-mm northern anchovy larvae were determined, using as criterion the incidence of two or more rotifers in the guts of 50% of larvae tested under different spectral irradiances. The threshold sensitivity to broadband blue-green light is at 0.15 $\mu Wcm^{-2} = 0.61$ lux. The action spectrum shows a maximum in the green wavelengths around 530 nm: the weighted threshold irradiances at various wavelength bands converge at a mean value of 0.14 $\mu Wcm^{-2}{}_{anch\ eff}$.

The visual abilities of the anchovy allow them to feed at a depth of 74 m at noon on clear days, and at the surface during twilight and bright nights, and appear to be well adapted to the anchovy's habitat in turbid, greenish coastal waters. Comparisons with younger anchovy larvae show that changes in visual function accompany changes in eye and retinal morphology, specifically the recruitment of rods. Moreover, 10-15-mm anchovy larvae can feed to a limited extent (10%) in the dark when food densities are high (20-40 rotifers/ml). In March, which is the peak spawning season of the anchovy in southern California and Baja California, the 10-15-mm larvae have 13 hours each day to feed.

RESUMEN

Se determina en larvas de *Engraulis mordax* (anchoa) de 10-15 mm. de longitud, el umbral de visibilidad para capturar alimento y la acción del espectro, usando como criterio la incidencia de dos o más rotíferos en el tubo digestivo del 50% de las larvas sometidas a estudio bajo diversas condiciones espectrales de radiación. La sensibilidad del umbral en la amplia banda de la luz verde y azulada se encuentra a los 0.15 $\mu Wcm^{-2} = 0.61$ bujías. La acción del espectro señala un máximo en las longitudes de onda de la banda verde, alrededor de los 530nm: la estimación del umbral de la anchoa en bandas de distinta longitud de onda, converge en un valor medio de 0.14 μWcm^{-2}.

La anchoa tiene una habilidad visual que le permite capturar alimento a una profundidad de 74 m. al mediodia en dias despejados, y en la superficie del mar al atardecer y en noches claras. Al parecer las anchoas se adaptan bien a su habitat de aguas costeras verdosas y turbias. Comparaciones efectuadas con larvas de anchoa más jovenes, indican que los cambios en la función visual corresponden con las variaciones en la morfología del ojo y de la retina, especialmente con la incorporación de los bastones. Las larvas de anchoa de 10-15 mm. de longitud, pueden alimentarse, con ciertas limitaciones (10%) en la oscuridad, cuando la densidad del alimento en el habitat es elevado (20-40 rotíferos por ml.). En el Sur de California y Baja California, el máximo de puesta de la anchoa se produce en Marzo, y entonces las larvas de 10-15 mm. de longitud disponen de 13 horas diarias de luz, que es suficiente para capturar el alimento.

INTRODUCTION

In this paper we determine the visual threshold and action spectrum of 10-15-mm northern anchovy (*Engraulis mordax*) larvae, and consider some implications of their feeding ecology. Studies on morphology and behavior have shown the importance of vision to anchovy (O'Connell 1963; Loukashkin and Grant 1965; Schwassmann 1965; Hunter 1972). At hatching, anchovy larvae are nearly transparent and have neither functional eyes nor jaws. O'Connell (1981) found that the oculomotor muscles differentiate at 3.5 mm SL; the photopic system is functional when feeding starts at 4 mm; and an area temporalis is present at 5 mm. The lens retractor muscle appears at 7 mm, and the rods at 10 mm. These developments indicate that an early feeding anchovy larva has a well-defined visual axis, good eye mobility, and binocular vision. The ability to accommodate to greater distances increases the perceptive field for feeding, and the recruitment of rods with commensurate increase in visual sensitivity increases the time that perception of food (and predators) is possible. Thus 10-mm anchovy can be expected to be more visually adept than 6-mm larvae. The ontogeny and maturation of sensory and locomotor systems and behavior patterns are important elements in larval survival (Hunter 1976a, 1977, 1981).

The visual threshold and action spectrum were de-

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[1] Present address: SEAFDEC Aquaculture Department, P.O. Box 256, Iloilo City, Philippines 5901

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termined to find out whether the morphological changes described above resulted in changes in visual function, and to obtain a basis for estimating the daily feeding period of larvae at sea.

MATERIALS AND METHODS

Anchovy larvae were reared at 16.5°-17.5°C from eggs spawned in the laboratory (Hunter 1976b; Leong 1971). Larvae grew to 10 mm in 3 weeks and then were transferred from the 300-liter rearing tank to 10-liter black plastic pots (30 cm dia, 10 cm deep), with 20-40 larvae in each pot. They were covered and kept in complete darkness for at least 12 hr to allow the guts to clear and the larvae to acclimate. Rotifers (*Brachionus plicatilis*) were used as prey because they are similar in size (180 μm) and optical density to most zooplankton and are easily cultured. Initially, we assumed that anchovy larvae could not feed in the dark, and the rotifers were added 12 hr before the tests at densities of 20-30/ml. When it became clear that some larvae could feed in the dark, the rotifers were added to the pots and dispersed just before the tests.

The apparatus, set in a darkroom, consisted of a completely sealed black box with three compartments, and three slide projectors (Kodak 600H with 127-mm f/2.8 lens with multimirror lamps GE ELH 300W, 120V) as light sources mounted 3 m away on the opposite wall (Figure 1). The three projectors were used simultaneously, their light beams isolated from each other by means of black cloth tubes. Slots in front of the lens held the various filters. In tests to determine the visual feeding threshold under broad-band blue-green light, we used a green glass filter (Schott BG-18) in combination with a 1-cm-thick glass cell filled with 5% copper chloride ($CuCl_2$) solution to approximate the spectrum at 20-m depth in waters with 0.8 mg Chl *a* m^{-3}. The color filters used for the action spectrum treatments were glass-mounted Kodak Wratten gelatin filters that selectively transmitted wavelength bands 60 to 112 nm wide with varying peaks (Table 1; Figure 2). Kodak neutral density absorption filters, calibrated with the spectroradiometer, were used to reduce intensities in logarithmic steps, nominally −0.5, −1.0, and −2.0.

A spectroradiometer (Optronic Laboratories 741V) interfaced with a Hewlett-Packard calculator-plotter was used to measure the spectral irradiance from 362 nm to 800 nm of each color filter at the level of the water surface of the test pots. This instrument was not sensitive to irradiance levels lower than the maximum projector output through each color filter; consequently, lower test irradiances were computed from the energy integral of the color filter multiplied by the transmission ratios of the neutral-density filters used.

TABLE 1
Filter Characteristics

Filters	Peak wavelength (nm)	Bandwidth[a] (0.01; in nm)	Irradiance[b] (μWcm^{-2})
Kodak Wratten			
18A + $CuCl_2$[c]	370	334 to 402; 68	0.80
47B	440	386 to 498; 112	15.22
75	485	458 to 540; 82	8.81
74	530	502 to 582; 80	11.53
73	570	552 to 612; 60	3.46
72B	600	582 to 650; 68	5.20
Schott			
BG-18 + $CuCl_2$	540	380 to 632; 252	153.0

[a] The wavelength range of the 1% bandwidth is identified as that portion of the spectrum spanned and as its width (in nm).

[b] Means (without neutral density filters) of 9 measurements for each color filter and 20 for BG-18.

[c] $CuCl_2$ (copper chloride cell) was used to reduce the transmission of red wavelengths from the projector lamp.

In this paper the feeding response is expressed as a function of irradiance (in μWcm^{-2}), the amount of energy that a unit surface of water intercepts from the light source directly above it, integrated over the wavelength band. To compare our results with those in the literature, we converted these into photometric units (lux) by weighting the spectral irradiances of the filters (Figure 2) against the standard luminosity curve for the human eye.

Eight treatments with eight filter combinations were made in one day, together with a bright control and a dark control. A bright control was exposure of larvae to unattenuated blue-green light from the projector (average irradiance at the water surface 153 μWcm^{-2}); whereas a dark control was completely sealed from light. Treatments consisted of exposure of 10-20 healthy 10-15-mm larvae and about 20-30 rotifers/ml to various spectral irradiances for 1.5 hr. After this interval and with the use of a small flashlight, we poured the larvae onto 300-μm plankton net filters; this almost instantly removed the larvae from water and minimized if not totally prevented defecation. The larvae were then spread on a glass slide. The gut contents were counted under a dissection microscope, a relatively easy operation given the larvae's transparent bodies and straight guts. The larvae were scored positive for incidence of two or more rotifers in the gut. The feeding incidence was used as measure of the larvae's response to differences in prey visibility.

Early in the experiment, we noted that the guts of 10-15-mm anchovy larvae in dark controls were not always empty but that 14.5% of them contained one or more rotifers. This observation ran counter to results under similar conditions for younger (6 mm) larvae (Hunter, unpublished data) and needed to be verified. Groups of 20-40 larvae were transferred into pots,

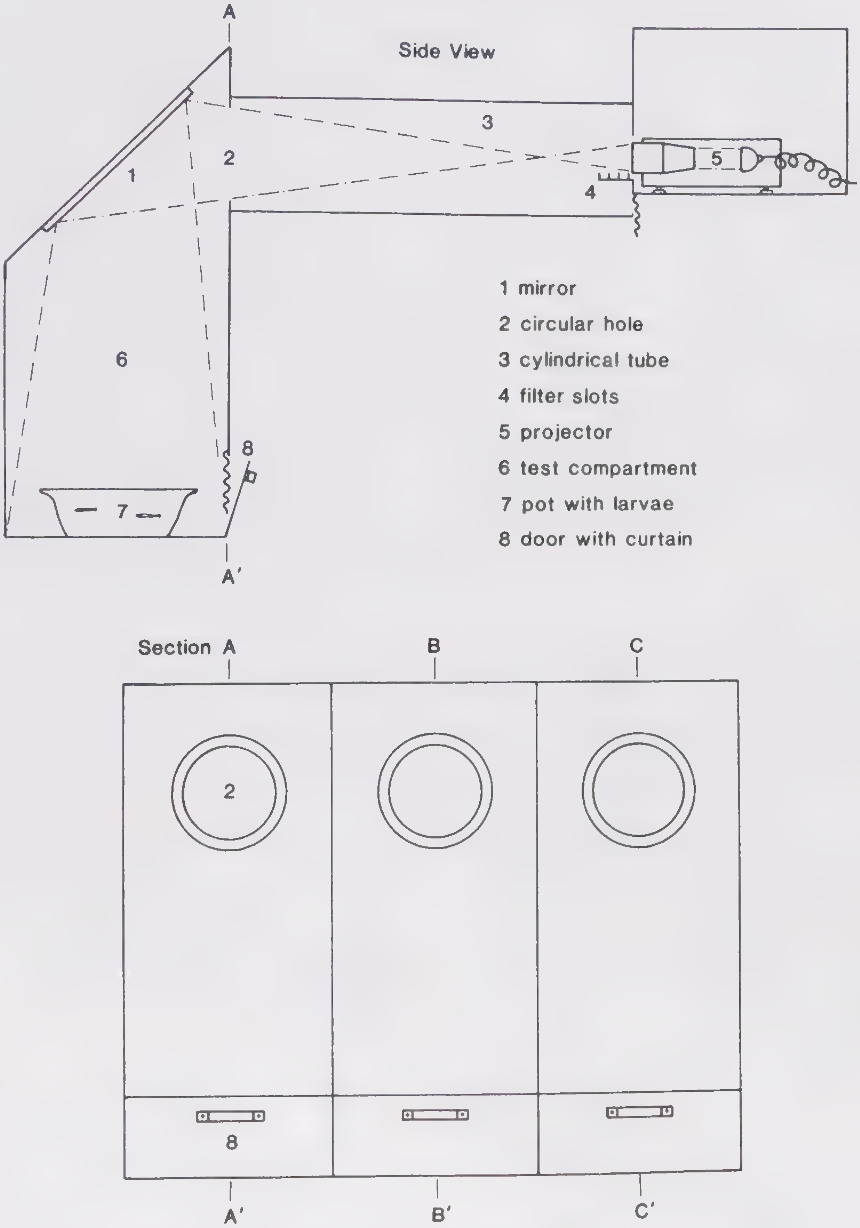

Figure 1. Apparatus for determining the visual thresholds for feeding of 10-15-mm anchovy larvae.

given or not given rotifers, then kept in darkness for different time intervals (from 30 min to 27 hr) and subsequently examined for incidence of food in the guts.

In the analysis of the light experiments, we adjusted the feeding incidence percentages for what turned out to be 10% feeding incidence in the dark (using the criterion of two or more rotifers/gut). Data were submitted to probit analysis (Finney 1971) to determine the irradiance for the 50% feeding thresholds (FT_{50}), under various spectral compositions of light. These FT_{50}'s were used to draw the action spectrum.

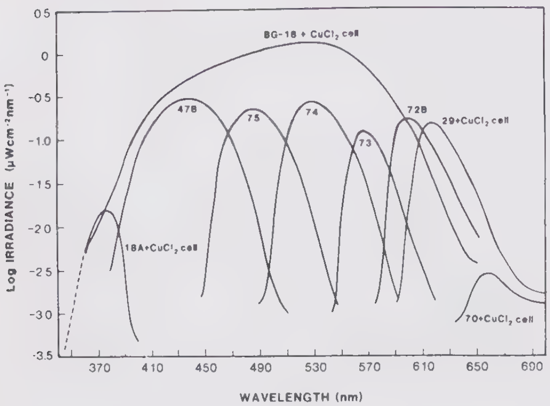

Figure 2. The spectral irradiance of the color filters used in the experiment. Filters used are given at top of each curve. All are Kodak with the exception of the Schott BG-18. BG-18 + $CuC1_2$ is the filter used for the broadband blue-green light treatments. The other filters are color filters, with maxima (from left to right) of 370 nm, 440 nm, 485 nm, 530 nm, 570 nm, 600 nm, 620 nm, and 660 nm. The irradiance below 362 nm in 18A is estimated from the curve drawn by eye (dashed).

RESULTS AND DISCUSSION

Visual Feeding Threshold under Blue-Green Light

Under bright control conditions, average irradiance 153 μWcm^{-2}, nearly all larvae fed (97.4 ± 1.7%, 36 tests, 475 larvae). This irradiance was equal to that in the rearing tank (150 μWcm^{-2}), where all larvae fed optimally. In most tests, the larvae were gorged with rotifers. The intestines must be very distensible because we once counted 240 rotifers in one gut, many still alive. Usual counts of full guts ranged from 20 to 100 rotifers per larva.

Figure 3 shows plots of the feeding incidence under blue-green light at eight log irradiance levels. The two graphs illustrate how the probit transformation linearizes the sigmoid relation. The probit regression line indicates that the 50% feeding threshold (FT_{50}) under blue-green light is 0.15 μWcm^{-2}, which is equal to 0.61 lux. This value is about one-tenth the threshold irradiance required by 6-mm larvae (FT_{50} = 1.6 μWcm^{-2} = 6.5 lux; Hunter unpubl.). Thus 10-15-mm larvae with both rods and cones are ten times more sensitive to prey than the 6-mm-larvae with cones only. This difference is probably even greater, because the criterion used for positive response was one or more rotifers per gut in the latter, whereas we used a criterion of two or more per gut.

This ten-fold increase in visual sensitivity, based on the feeding response, of 10-15-mm anchovy relative to 6-mm larvae is very probably related to the recruitment of rods and not to improvements in feeding efficiency. The feeding success of anchovy larvae does not change much as they grow from 6 mm to 10-15 mm (Hunter 1972). The proportion of time spent searching for food and the maximum ingestion rates of 6-mm larvae differ little from those of 10-15-mm larvae. The improvement in visual sensitivity may also be due to other developmental changes in the retina, including increase in the number of visual cells and neural connections, the differentiation of the retractor lentis, and greater production of visual pigments.

The visual feeding threshold of anchovy larvae is similar to the thresholds of other fish larvae (Table 2). Some variability in the thresholds exists, depending on the species; the criteria used; the age of the fish (length, presence of rods, degree of motor development); and the type, visibility, and size of prey. Prey density affects feeding thresholds, but few of the studies enumerated gave the densities used.

A more direct comparison between the thresholds for anchovy and herring can be made. Blaxter (1966) detected 10% feeding incidence for 12-14-mm herring at 0.13-0.19 lux. The probit regression line (Figure 3) can be used to estimate the irradiance level at 10% feeding incidence in 10-15-mm anchovy larvae, and this is 10^{-4} μWcm^{-2} or 0.0004 lux. It thus seems that anchovy larvae are at least 100 times more sensitive than herring larvae of similar size. More accurately perhaps, anchovy larvae at 10-15 mm are more advanced developmentally than are herring larvae at 12-14 mm. The adult northern anchovy may have even greater sensitivity than the larvae, considering the special characteristics of its retina and eye (O'Connell 1963). At zero feeding incidence (Figure 3), the irradiance is equivalent to about 10^{-7} lux, which may be close to the absolute threshold of anchovy rods. Protasov (1964) found that the threshold light sensitivity of the adult Mediterranean anchovy (*Engraulis encrasicholus*) as determined by the electroretinogram is at 10^{-8} lux.

Action Spectrum for Feeding

Figure 4 shows the feeding incidence under different spectral conditions plotted on probit scale against log irradiance. The 50% feeding threshold irradiances (FT_{50}'s) are indicated. The lowest irradiance that elicits 50% feeding occurs around 530 nm, whereas much more energy is required around 370 nm and 660 nm. The 95% confidence intervals (horizontal bars) of the FT_{50}'s cover about one order of magnitude, except for the two extreme wavelength bands. In the latter, larger errors occurred because the 50% feeding thresholds had to be extrapolated beyond the range of data (as indicated by the dotted portions of the regression lines for 370 nm and 660 nm in Figure 4). This was because the apparatus did not produce sufficient

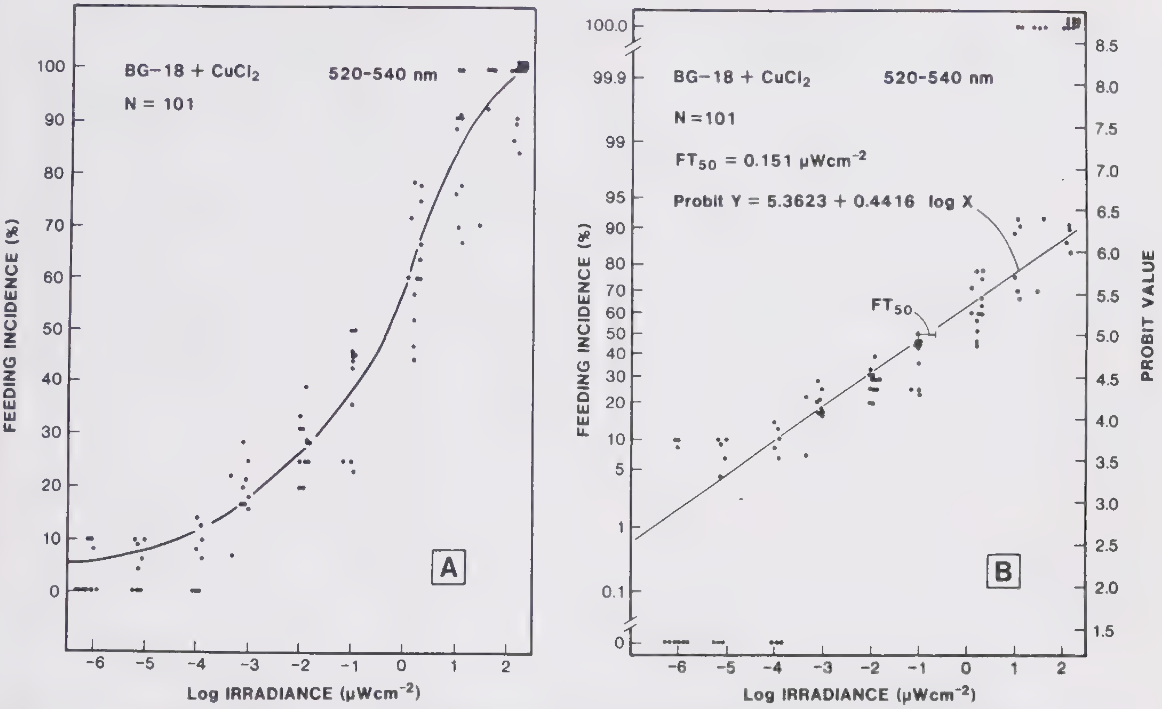

Figure 3. The incidence of feeding (percentage of larvae with two or more rotifers in the gut) under various irradiance levels of blue-green light. FT_{50} is the 50% feeding threshold; the horizontal bar indicates the 95% confidence interval using probit analysis (Finney 1971); N, the number of tests. In both graphs, the abscissa is on log scale; the ordinate is on linear scale in *A* and probit scale in *B* (with probit values given at the right.) The equation gives the regression of y = probit value on x = log irradiance.

TABLE 2
Visual Thresholds for Feeding in Fishes

Species	Length stage	Feeding threshold	Criteria	Prey	Author
Northern anchovy	6 mm	6.5 lux	50% larvae with R≥1	*Brachionus*	Hunter (unpubl)
	10-15 mm	0.6 lux	50% larvae with R≥2	*Brachionus*	This study
Herring	12-14 mm	0.13 lux	10% feeding incidence	*Artemia*	Blaxter (1966)
	12-14 mm	0.19 lux	10% feeding incidence	*Balanus*	Blaxter (1966)
	13-17 mm	0.02-0.09 lux	Number of prey taken extrapolated to zero	*Artemia*	Blaxter (1968a)
	13-17 mm	0.10-0.18 lux	Number of prey taken extrapolated to zero	*Balanus*	Blaxter (1968a)
	90-100 mm	0.036-0.007 lux	Cessation of feeding	Squid	Blaxter (1964)
Plaice	6 mm	1-10 lux	Feeding index reduced to 10%	*Artemia*	Blaxter (1968b)
	9-15 mm	0.01 lux	Feeding index raised above dark level	*Artemia*	Blaxter (1968b)
	6 mm	0.01-1 lux	Feeding index reduced to zero	*Artemia*	Blaxter (1969)
Cod	4-5 mm	0.1-0.4 lux	0 feeding incidence	*Artemia*	Ellertsen et al. (1980)
Jack mackerel	93-143 mm	6×10^{-7} ft-L	Incidence of prey in fish gut	*Artemia*	Hunter (1968)
	93-143 mm	6×10^{-5} ft-L	Incidence of 50% of prey taken in light	*Artemia*	Hunter (1968)
Pacific salmon	Young	10^{-4} ft-c	50% available prey eaten	*Daphnia*	Brett and Groot (1963)
	Fry/smolt	10^{-5} ft-c	Feeding extinguished	*Daphnia*	Ali (1959)
	Fry/smolt	0.1-1 ft-c	Feeding reaches maximum	*Daphnia*	Ali (1959)

R is the number of rotifers in the guts of anchovy larvae; 1 ft-c = 10.764 lux; under scotopic conditions, ft-c approximately equal to ft-L

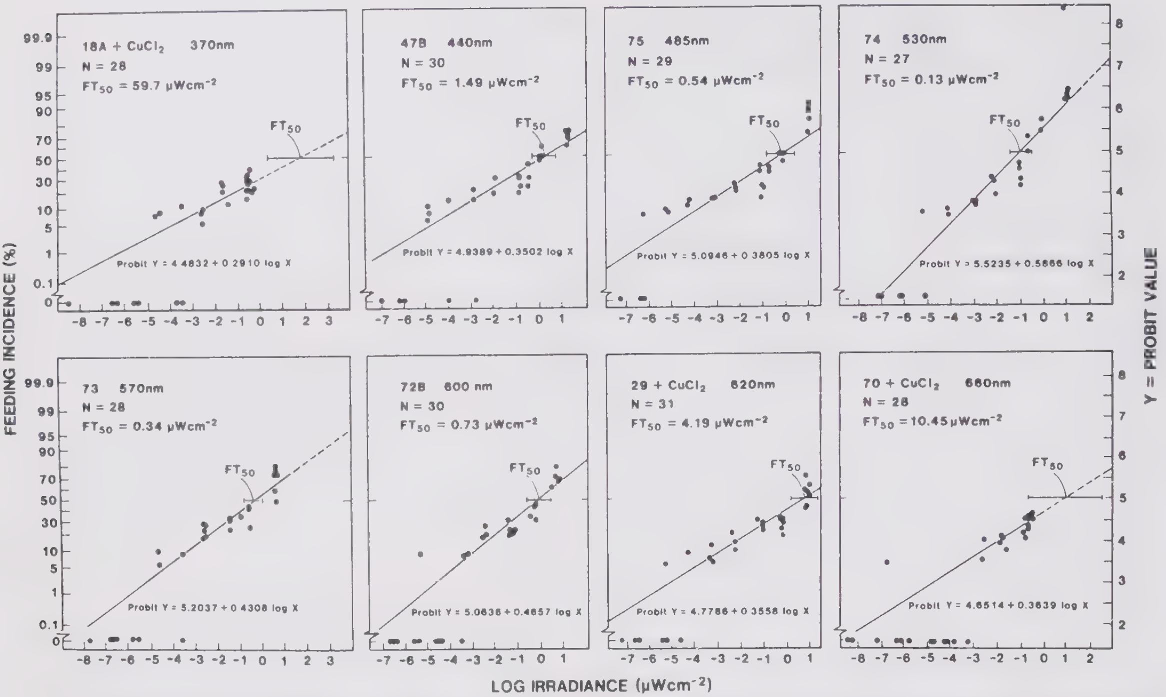

Figure 4. The incidence of feeding (percentage of larvae with two or more rotifers in the gut) under various wavelengths and irradiance levels. The filter name and peak transmission wavelength are given at the top left-hand corner. FT_{50} is the 50% feeding threshold using probit analysis (Finney 1971) (the horizontal bars indicate the 95% confidence intervals); N, the number of tests. All graphs are on logarithmic scale abscissa and probit scale ordinate (probit values at the right). Equations give the regression of y – probit value against x = log irradiance. The corrected FT_{50} for 18A is 27.7 μWcm^{-2}, and this value was used in the action spectrum.

energy to induce a 50% response at these wavelengths. The higher uncertainty at the extreme wavelengths should not detract from the overall accuracy of the action spectrum. Since the eye is essentially a log receptor, ± ½ log unit for most points is adequate precision.

Spectral sensitivity is usually expressed as the reciprocal of the threshold radiant energy. In Figure 5, we plot $1/FT_{50}$ in μWcm^{-2}, as well as in equivalent 1/photon units, to give the spectral sensitivity curve of 10-15-mm anchovy larvae. The number of photons at threshold level was obtained by multiplying the FT_{50} by the number of photons per erg at the peak wavelength (Withrow and Withrow 1956). The sensitivity curve in photons is displaced relative to that in energy units because the energy content per photon is higher in the short than in the long wavelengths. Either curve can be considered as the action spectrum of 10-15-mm anchovy for feeding on translucent prey; peak sensitivity occurs at 530 nm. The relative sensitivity coefficients are indicated on the leftmost scale in Figure 5.

The anchovy action spectrum peaks decidedly in the green part of the spectrum—between 510 nm and 550

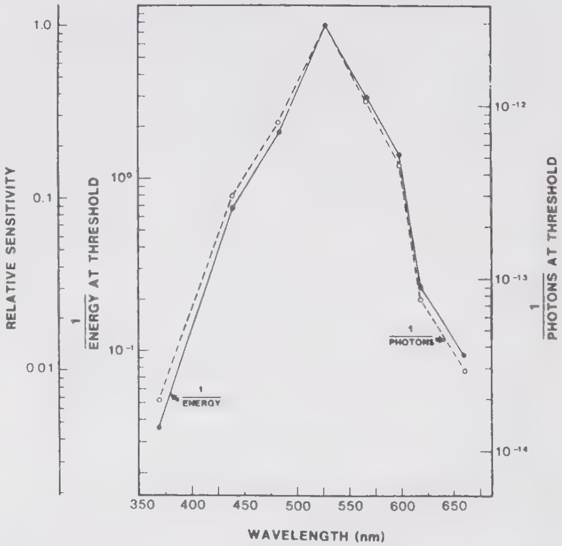

Figure 5. The action spectrum of 10-15-mm northern anchovy larvae for feeding on translucent prey, based on the reciprocals of the 50% feeding thresholds in energy and photon terms (given on log scales inside the graph). The leftmost log scale on the ordinate is the relative sensitivity of the anchovy at various wavelengths when the peak sensitivity at 530 nm is set equal to 1.0 and those at other wavelengths normalized accordingly.

nm. Northern anchovy are distributed off California and Baja California close to the coast. California waters transmit maximally in the green (Tyler 1961, 1964; Kampa 1961; Hobson et al. 1981). The larvae's increased sensitivity to green makes their environment appear relatively brighter and their prey easier to detect by contrast. The action spectrum obtained in this study may be applicable to most natural prey (primarily copepod nauplii to adults): like rotifers, they are often translucent.

Based on the FT_{50}'s, the action spectrum may be attributed to the rods, with some contribution from the cones. Most of the test irradiances were low (with energies quantitatively less than the blue-green light threshold), and in these the cones of the dark-adapted larvae were probably never activated. In the higher irradiance tests, both rods and cones may have been activated. The slopes of the probit regression lines for the various wavelength bands (Figure 4) were not homogeneous ($F=3.60$, $P=0.001$, $k=7$, $DF=215$) as they would have been if the response were due to only one visual system (rods only). Moreover, comparison of the northern anchovy larval action spectrum with the scotopic (with maximum at 500 nm) and the photopic (with maximum at 560 nm) ERG spectral curves of the adult Mediterranean anchovy (Protasov 1964) shows that it lies between the two values. The same is true in comparison with human luminosity curves. This also seems to indicate that the anchovy action spectrum for feeding has both rod and cone components.

If the form of the action spectrum were accurate, the energy at the 50% feeding incidence level would be the same value for all the spectral irradiances when these are weighted by the action spectrum. As a rough test of the action spectrum, we calculated the irradiance in anchovy effective units ($\mu Wcm^{-2}{}_{anch\ eff}$) by weighting the spectral irradiances of the various filters (Figure 2) using the anchovy action spectrum (Figure 5) and adjusting the 50% feeding thresholds. The weighted thresholds range in value from 0.10 to 0.17 $\mu Wcm^{-2}{}_{anch\ eff}$ and average 0.14 $\mu Wcm^{-2}{}_{anch\ eff}$ (Table 3). These tests are interesting but are not independent because the eight color filters were used to estimate the action spectrum. An independent test of the action spectrum for predicting 50% feeding incidence under different spectral irradiances is to convert the 50% threshold estimated under the broadband filter combination ($BG-18$ + $CuCl_2$) to anchovy effective units by weighting the spectral irradiance of the broadband filter by the anchovy action spectrum and comparing the results to the thresholds estimated for the other filters. Since the broadband filter was not used to estimate the action spectrum, this procedure is an independent measure of the accuracy of the action spectrum. Under the broadband filter the 50% feeding incidence threshold, in weighted units, was 0.076 $\mu Wcm^{-2}{}_{anch\ eff}$, which is different by only a factor of 2 from the average value for the other color filters (Table 3). Certainly this level of accuracy seems good, considering that the confidence interval around any point in the action spectrum was about an order of magnitude (Figure 4). This test indicates that the action spectrum obtained is a reliable predictor of the wavelength dependency of the feeding performance of anchovy larvae. This also means that, with an uncertainty of 2×, the feeding threshold can be estimated for any water type where the spectral irradiance is known, simply by weighting the irradiance by the action spectrum.

TABLE 3
Comparison of the 50% Feeding Thresholds (FT_{50}) under Different Spectral Conditions and Weightings

Peak wavelength (nm)[a]	Ratio[b]	50% feeding threshold: Unweighted FT_{50} μWcm^{-2}	50% feeding threshold: Weighted FT_{50} $\mu Wcm^{-2}{}_{anch\ eff}$[c]	50% feeding threshold: Lux
370	0.0060	27.7	0.1662	43.21
440	0.1053	1.49	0.1569	2.79
485	0.3428	0.54	0.1851	1.54
530	0.8678	0.13	0.1128	0.79
570	0.3931	0.34	0.1336	2.04
600	0.1358	0.73	0.0991	2.70
620	0.0348	4.19	0.1458	8.38
660	0.0139	10.45	0.1453	11.09
Blue-green (broadband)	0.5092	0.15	0.0764	0.61

[a] Peak of the spectral irradiances of the filters (Figure 2).
[b] Fraction of the filter spectral irradiance effective for anchovy feeding (obtained by weighting the former against the anchovy action spectrum).
[c] The ratio in column 2 times the 50% feeding thresholds (Figure 4) gives the irradiance in anchovy effective units $\mu Wcm^{-2}{}_{anch\ eff}$.

There appears to be a difference in the spectral sensitivity of 6-mm and 10-15-mm anchovy larvae tested under similar conditions. Younger larvae, which have cones only (O'Connell 1981), have a broader curve with two maxima at 440 nm and 600 nm (Hunter unpubl.), whereas the older larvae studied here have a narrow scotopic curve with maximum at 530 nm. This green sensitivity is also shown by adult anchovy (Loukashkin and Grant 1965). Blaxter (1964, 1968a) shows a similar development in herring: larvae with pure-cone retina have photopic curves with 1 to 3 maxima depending on the behavior and test conditions; the juveniles with rods show a scotopic maximum at 510-520 nm.

The action spectrum may be expected to reflect the absorption spectrum of the visual pigment. The visual pigment of northern anchovy has not yet been extracted but is probably similar to that of the deepbody anchovy, *Anchoa compressa*, a relative that also lives in turbid water and has an absorption maximum at 510 nm (Munz 1957). The action spectrum of 10-15-mm northern anchovy is similar to that of juvenile herring (Blaxter 1964), to the scotopic ERG spectra (with maxima at 520-540 nm) of several species of shallow-water marine and freshwater fishes studied by Kobayashi (1962) and Protasov (1964), and to the scotopic sensitivity spectrum (with peak at 525 nm) of adult *Tilapia* (Tavolga and Jacobs 1971).

Feeding in the Dark

Of the larvae kept 12-24 hr in the dark, 12% had two or more freshly ingested rotifers in the gut at high food densities (40 rotifers/ml) whereas only 3% fed in pots where the only food present was that transferred with the larvae from the rearing tank (5 rotifers/ml) (Table 4). There was no doubt that most of the food seen in the gut was recently consumed because many of the rotifers were undigested, and Theilacker (Southwest Fisheries Center, La Jolla, pers. comm.) found that the time for complete evacuation of the gut in feeding anchovy larvae less than two weeks old, as well as in herring larvae up to five weeks old, varied little from 2 hr. That the incidence of food in the gut showed a significant increase at high food densities ($x^2=11.53$, $p=0.007$ when the criterion used is two or more prey per gut or $R \geq 2$) also clearly demonstrates that 10-15-mm larvae can feed in the dark at high food densities. The dark controls with 20-25 rotifers/ml averaged 10% feeding incidence (Table 4). It appears that the extent of dark feeding depends on the food density.

Previous work on larvae of the northern anchovy and related species has shown a marked diurnality in feeding activity, with no feeding in the dark (Berner 1959; Arthur 1976). Arthur, however, mentions a remarkable "exception": a sample taken 38 km off the coast of central Baja California approximately 6 hr after sunset and 1.5 hr after moonset (first quarter moon) contained both anchovy and sardine larvae literally crammed with the pteropod *Limacina bulminoides*. Mollusks were otherwise a rare item in the guts of these larvae. O'Connell (1981) found that the olfactory and the lateral line apparatus are present and apparently functional at hatching in anchovy; maturation of these systems continues throughout larval life. These faculties are sufficiently developed to be used by the larvae in locating prey in the dark. Olfaction may be used to locate prey patches; once in a patch, larvae could ingest food by swimming through open-mouthed or by blindly striking.

Dark feeding has been observed in other fish larvae, (Blaxter 1969; Bainbridge and McKay 1968; John and Hasler 1956; Ellertsen et al. 1980). Blaxter (1966) noted that some of the 12-14-mm herring larvae (without rods) in his dark controls fed overnight. Dempsey (1978) showed that herring respond by olfaction to washings and extracts of prey they had previously fed on, and to amino acids characteristic of these prey. Herring larvae with the eyeballs removed are able to feed at very high food densities (Hunter personal observation).

TABLE 4
Feeding Incidence in Anchovy Larvae Kept 12 hr or More in the Dark

Rotifer density (#/ml)	Number larvae	Number tests	Feeding incidence Mean ± (2SE) (%)	
			$R \geq 1$[a]	$R \geq 2$
5	188	21	10.74 (5.90)	2.89 (2.41)
40	172	21	26.99 (6.92)	12.44 (5.80)
22[b]	428	37	14.49 (4.28)	9.41 (3.41)
25[c]	140	10	14.16 (7.13)	10.10 (4.29)

[a] R is the number of rotifers in the guts of larvae; $R \geq 1$ is the original, and $R \geq 2$ the modified criterion of positive feeding incidence applied to the same larvae.

[b] Dark controls for the threshold experiments in which rotifers were added 12 hr before test.

[c] Dark controls in which the rotifers were added just before test. The chi-square test shows significant differences in the frequencies of feeding larvae under low and high food density conditions: $X^2 = 11.53$, $P = 0.007$ when $R \geq 2$, and $X^2 = 20.66$, $P = 0.001$ when $R \geq 1$.

Daily Feeding Period

One of the important effects of increased visual sensitivity is the increase in the length of time that larvae are able to feed effectively (Blaxter 1966). When the sun is 6° below the horizon (civil twilight), illumination at the sea surface is about 3.4 lux (Brown 1952). This irradiance level would still enable 50% of 10-15-mm anchovy to feed, but is below the feeding threshold of the 6-mm larvae. Full moon is typically 0.1 lux, and at least some 10-15-mm larvae could feed at the surface. The broadband blue-green feeding threshold of 10-15-mm anchovy larvae, 0.15 μWcm^{-2} = 0.61 lux = 0.057 ft-c, is reached at the earth's surface when the sun is 7.5° below the horizon at dusk and dawn. With the sun 6° below the horizon, we calculate that in California waters with a total attenuation coefficient of 0.152/m in January (Tyler 1961), 50% of 10-15-mm anchovy larvae could still feed at 5-m depth. At noon of a typical sunny day, when incident illumination is 11,500 ft-c at the surface (Brown 1952), 50% of 10-15-mm anchovy could feed at 74 m. Anchovy larvae are distributed from the surface down to about 100 m, with about 95% of them in the upper 60 m (Ahlstrom 1959). Larvae 10 mm and larger remain near the surface at night and descend to

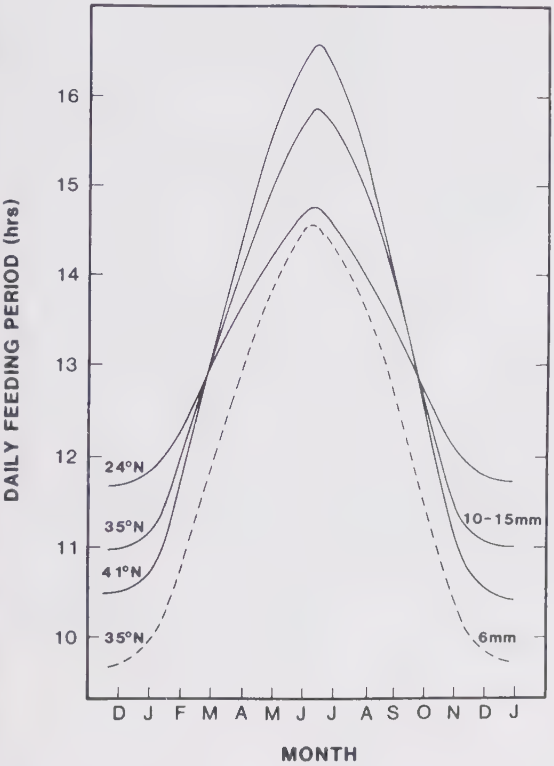

Figure 6. The daily feeding period of anchovy larvae at these selected latitudes at different times of the year.

depths down to 70 m in the day (Hunter and Sanchez 1976).

We calculated the daily feeding period of anchovy larvae (the number of hours when the light intensity at the sea surface is above the visual threshold value and the larvae are able to feed) based on Brown's (1952) Natural Illumination Charts. Figure 6 shows the daily feeding periods of 10-15-mm anchovy larvae at 41°N (Cape Mendocino), 35°N (Point Concepcion), and 24°N (Point San Juanico). It appears that in southern Baja California there is sufficient light for feeding by 10-mm anchovy larvae for 12 or more hours per day throughout the year. Southern California larvae have at least 11 hr and up to 16 hr per day. The anchovy population that occurs north of Cape Mendocino into Canada spawns in the summer, at which time there are 17-18 hr for larvae to feed (and the temperature and the food supply are favorable).

At 35°N, 10-15-mm larvae have approximately one hour more each day for feeding than the 6-mm ones, a consequence of their higher visual sensitivity. Thus, contrary to Hunter's (1972) assumption of a 10-hr feeding day, anchovy larvae have potentially much longer daily feeding periods. In March, which is the peak spawning month, 6-mm larvae can feed about 12 hr and 10-15-mm larvae 13 hr each day. This, of course, increases the possible volume of water searched by 10-15-mm larvae per day by 30% and thereby improves the chance of finding food by that amount.

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SEA TURTLES AND THEIR TRADITIONAL USAGE IN TOKELAU

BY

GEORGE H. BALAZS*

ABSTRACT

The conservation status, ecology, and cultural importance of sea turtles at the three Polynesian atolls of Tokelau are presented. The green turtle, Chelonia mydas, is the most common species, occurring as a migrant breeder mostly during September through November. The hawksbill, Eretmochelys imbricata, is present in small numbers at all three atolls, but nesting is only known at Nukunonu Atoll. A third species, the loggerhead, Caretta caretta, has also been recorded on rare occasions. In Tokelau, sea turtles are considered "sacred fish" (ika hā) that must be shared among the entire village by an equitable system known as inati. The number of sea turtles has declined within historical times apparently as a result of modern and more efficient hunting methods.

A main objective of this research is to help the Tokelauans effectively manage sea turtles so that these animals can continue to be part of the native diet and culture. Based on this study's findings, 11 recommendations for conservation are offered that either build upon, or reinforce, existing traditional practices. These conservation measures may also be applicable to sea turtle populations used by other insular people of the Pacific.

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*Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, P. O. Box 3830, Honolulu, Hawaii 96812

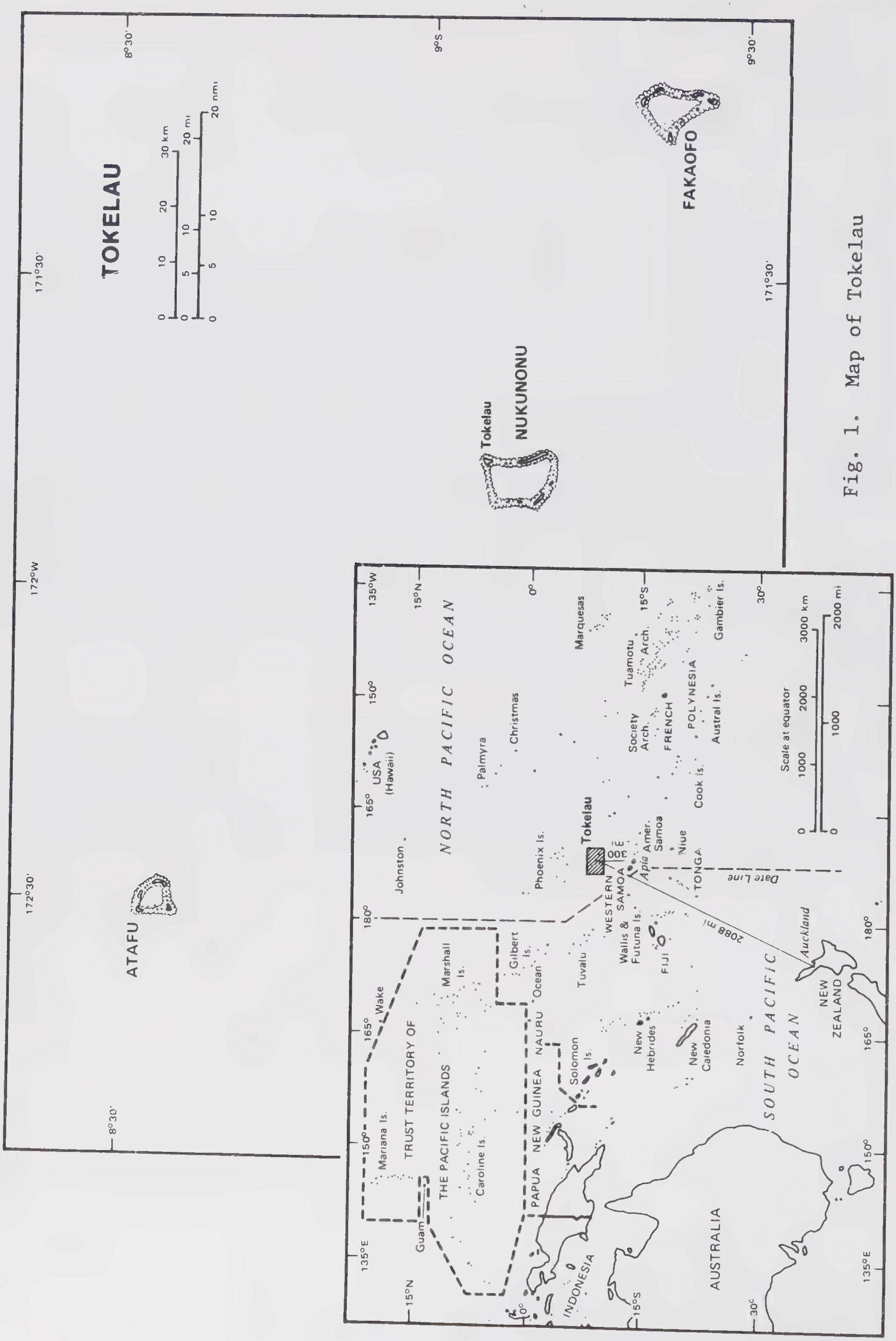

Fig. 1. Map of Tokelau

INTRODUCTION

This paper presents results of a field study undertaken in October of 1981 to assess the status, ecology, and human usage of sea turtles at the three Polynesian atolls of Tokelau in the central South Pacific Ocean. The ultimate aim of this study is to work in harmony with the native people to help conserve the area's sea turtles so they will continue to be part of the Tokelauan diet and culture.

The method being pursued to achieve this objective is to build upon existing traditional conservation practices, while taking into account the current biological knowledge of sea turtles and the legitimate needs of island people striving for an improved life. The need for such efforts in the Pacific is considerable. To a great extent, the numerous small islands of Polynesia, Micronesia, and Melanesia share the common problems of being extremely limited in natural resources and isolated from the outside world. These factors are even more pronounced on low coral atolls with small human populations. The Tokelau group is in many ways representative of such circumstances, where subsistence living is carried out in a remote island environment. Numerous changes have been brought about by outside influences over the past 125 years, but the basic cultural bonds and sense of unity among the people remain intact. There is a desire to retain many of the traditional ways of life, while selectively incorporating new ideas and more material goods and services into the culture. To maintain the necessary balance, it is essential that the environmental components upon which the culture depends remain viable. Sea turtles are one of these elements that constitute a high-protein seasonal food source offering welcome variety to the native diet. The capture, preparation, and sharing of turtles also serve as a social function that helps to strengthen and enrich the village community.

Sea turtles were formerly of considerable importance to many Pacific islanders. In addition to being a prized and nutritious food, they played key roles in certain religious ceremonies held at stone structures built on their behalf (Buck 1932a, 1932b; Emory 1947). The scutes and bones of turtles were used to fashion decorative ornaments, fishhooks, tattoo needles, and a variety of other implements. Sea turtle motifs were incorporated into petroglyphs and other works of art, as well as songs, dances, and folklore (Burrows 1933; Emory 1933; Pukui and Elbert 1971).

The decline in the importance of sea turtles within Pacific island cultures can be attributed to a number of factors, one of which is the decline of the resource itself. At many islands, traditional conservation methods that buffered turtles and other marine resources from overexploitation have deteriorated considerably, and in some cases disappeared completely. Three interrelated factors identified by Johannes (1978) that have contributed to this breakdown include the introduction of money economies, the decline of traditional authority, and the imposition of new laws and practices by foreign powers. The available evidence shows that the numbers of turtles throughout the Pacific islands have decreased markedly during historical times. However, for some areas no documentation exists on former levels of abundance and nesting distribution. Such information urgently needs to be gathered from the elders of each island before it is lost. A greater overall effort needs to be undertaken to conserve Pacific sea turtles, in collaboration with the people that are culturally linked to them. There is already a growing awareness of the problem, as demonstrated by recent reports and actions recommended (South Pacific Commission/National Marine Fisheries Service 1980; World Conference on Sea Turtle Conservation 1980). Also, information presented in McCoy (1974) and Pritchard (1977) for Micronesia, Balazs (1980) for Hawaii, Vaughan (1981) for the Solomon Islands, and Hirth (1971), Balazs (1977), and Dahl (1980) for Pacific islands in general, provides a basis for expanding and refining sea turtle conservation studies in the Pacific.

The study reported herein focuses attention on three atolls that are believed to be representative of many small islands scattered across the Pacific. Because of funding and other limitations, it will probably never be possible to carefully investigate the interrelations of turtles and people at all of these locations. I therefore plan to continue using Tokelau as a model study area, with the monitoring and cooperative assistance being carried out through fishermen, village elders, and other authorities that I met during my visit.

TOKELAU

Physiography

Tokelau consists of three coral atolls named Fakaofo, Nukunonu, and Atafu located between lat. 8° to 10°S and long. 171° to 173°W (Figure 1). The islands lie in a straight path extending from southeast to northwest. Fakaofo, the southernmost island, is 65 km from Nukunonu and 150 km from Atafu, the northernmost island. The group is about 500 km north of Upolu and Savai'i, the two large volcanic islands that comprise the independent nation of Western Samoa. The nearest neighbors to the west of Tokelau are the atolls of Tuvalu, which are about 650 km away. The atolls of the northern Cook Islands are situated to the east of Tokelau. Pukapuka, the closest of the group, is 500 km away. Gardner, Hull, and Sydney, three atolls in the Phoenix group (part of Kiribati), are about 450 km to the north of Tokelau, but all are currently uninhabited. Swain's, a 2-km long coral island known to the people of Tokelau as Olosega, lies 175 km south of Fakaofo. This island has historic cultural ties with Tokelau; however, since 1925 it has been a territory of the United States under the administration of American Samoa. Only about 15 people now live on Swain's Island.

The atolls of Tokelau consist of reefs that encircle large lagoons that lack a deepwater passage. Waves break on these protective reefs and flow over into the lagoon where relatively calm waters prevail. Many of the reefs are entirely bare during periods of low tide. On the ocean side of the reef the bottom drops off rapidly to great depths just a short distance from shore. Numerous islets (motu) ranging up to 6 km long, 400 m wide, and 5 m above sea level are located along the reefs. The motu soil is composed of coral sand and rubble generally low in organic matter. The principal vegetation cover consists of coconut palms, _Cocos_, along with _Pandanus_, _Scaevola_, and _Tournefortia_. Other noteworthy native plants include _Cordia subcordata_ (kanava), _Pisona grandis_ (pukakakai), _Pemphis acidula_ (ngagie), _Hernandia nymphaeaefolia_ (pukavaka), and _Morinda citrifola_ (nonu). The estimated total land area of each atoll is 250 ha for Fakaofo, 260 ha for Nukunonu, and 205 ha for Atafu.

The southeast trade winds prevail in Tokelau from April to September, and northerly or variable winds prevail during the remaining hotter months of the year. The average temperature is 28°C and the average annual rainfall about 290 cm. Precipitation is greater during the months of October through March. Wells have been dug at each atoll, but most drinking water is obtained from coconuts and the collection of rainwater. Hurricanes are not common, but can cause great damage when they pass through the area. Severe storms are known to have hit Tokelau in 1846, 1914, and 1966.

Some good overall accounts of the physiography of Tokelau can be found in Macgregor (1937), Bryan (1942), Great Britain Naval Intelligence (1943), and Hooper and Huntsman (1973). Published information on the biota of Tokelau is available for the topics of seabirds (Wodzicki and Laird 1970), rats (Kirkpatrick 1966; Mosby and Wodzicki 1973), lizards (Whitaker 1970), arthropods (Hinckley 1969; Yaldwyn and Wodzicki 1979), and vegetation (Parham 1971; Whistler 1981). Wiens (1962) provides a comprehensive treatise on the environment and ecology of atolls in general, including some specific aspects of Tokelau.

Historical Overview

The discovery of Tokelau by European and American seamen started in 1765 with the sighting of Atafu. Nukunonu was discovered in 1791, but Fakaofo was not found until 1835. During the mid-1800's Christian missionaries became established on all three islands. In the 1860's the population was substantially reduced by the introduction of epidemic diseases and kidnapping by Peruvian slavers. Several foreign traders, mainly of Portuguese descent, settled in the islands during the latter 1800's and, through intermarriage, established family lines that continue to the present-day Tokelauans. A number of other ethnic groups were also absorbed into the genetic makeup of the population.

In 1877 the islands were placed under British protection and in 1916 Britain annexed the group. At that time Tokelau was known as the Union Islands. In 1925, responsibility for Tokelau was transferred to the New Zealand Government with administration being carried out from

Western Samoa. In 1948 the islands were formally incorporated as a territory of New Zealand. This status continues to the present with Tokelauans being full citizens of New Zealand. The group's external matters are handled by the Office for Tokelau Affairs based in Apia, Western Samoa.

An interesting event in the history of Tokelau that seems to be missing from the available literature is that a small U.S. Coast Guard loran station existed on Atafu in 1944 as part of the Pacific war effort.

The People

The Tokelauans are a stock of Polynesians that share a common language, culture, homeland, and way of life. The origin and early settlement of the islands are not clearly known; however, certain similarities exist with each of the surrounding Polynesian cultures. The traditional histories of Tokelau suggest separate founding populations at each atoll, and record the subsequent hegemony of Fakaofo by driving off the "true" Atafuans and conquering the people of Nukunonu. Atafu was not resettled until about 1800. Fakaofo's dominance was symbolized by the location of the temple and stone effigy of Tui Tokelau on that island (J. W. Huntsman, personal communication in April 1982).

Since the turn of the century the affinity with Samoan culture has increased in Tokelau due to such factors as greater travel opportunities on supply ships from Apia, use of the Samoan Bible, and broadcasts by Samoan radio stations. The Tokelauan language of the Polynesian family has only been written for about the past 15 years.

The population of Tokelau within historic times was reduced to a low of 200 in the 1860's, and reached a high of nearly 2000 during the 1960's. Emigration has occurred over the years, some of which was stimulated by a desire for wage employment and the limitations of natural resources, especially following the hurricane of 1966. There are now about 2500 Tokelauans living permanently in New Zealand, a few hundred in Western Samoa, and at least 150 in Hawaii (see Cooke 1975). This latter group originated from contract laborers on Swain's Island who were able to travel to American Samoa, and later north to Hawaii. The current population of Tokelau is approximately 1600, including about 675 people on Fakaofo, 350 on Nukunonu, and 575 on Atafu.

The people at Nukunonu and Atafu all live in a single village whereas at Fakaofo a second motu has been populated due to crowding at the historic village site. Each atoll operates as a relatively separate social unit since there is no transportation between islands except when a supply ship comes from Apia. During 1981 there was approximately one ship every 2 months.

Life in Tokelau is organized around kinship groups known as kāiga. Daily activities involve various forms of fishing and the harvesting of food crops, including coconuts that are dried into copra for export.

Groups of men must regularly travel to the outlying uninhabited motu of the atoll to gather coconuts. The majority of the food consumed is obtained locally from the atoll and the surrounding ocean. In addition to coconuts, other basic food crops are breadfruit, pandanus, and pulaka, Cyrtosperma chamissonis. Pigs and chickens have been introduced to the village motu and provide supplemental sources of animal protein, usually reserved for special occasions.

Tokelau society is traditionally egalitarian in ethic and cognatic in terms of descent and inheritance. Each atoll is governed by a Council of Elders (taupulega) representative of the kāiga groups. In addition, a village commissioner (faipule) and mayor (pulenuku) serve as elected officials. Close family ties exist in Tokelau and there is great respect for the aged.

Comprehensive information on the ethnology of Tokelau has been assembled by Burrows (1923) and Macgregor (1937). Detailed studies of the demography, kinship relations, and other cultural aspects of Tokelau have been published during recent years by Huntsman (1971, 1977), Hooper and Huntsman (1973), and Huntsman and Hooper (1975, 1976). An enlightening popular account of life in Tokelau has been produced by the New Zealand Department of Education (Keen 1976).

Sea Turtles

Very little information has been published on the status and ecology of sea turtles in Tokelau. The available material can be summarized as follows.

In a consultancy report on turtle resources of the South Pacific, Hirth (1971), based on an interview with Dr. J. Huntsman, stated that "Green turtles [Chelonia mydas] and to a much lesser extent hawksbills [Eretmochelys imbricata] still nest in the Tokelau Islands (September - October) but their numbers are said to be rapidly decreasing." Wodzicki (1972) indicated that "Five species of marine turtles lay their eggs on the beaches [of Tokelau], and in the past used to be an important food item for the islands but unfortunately have lately been very low in numbers." In a later paper, Wodzicki (1973) again briefly mentioned five species being present, and added that "turtle nesting grounds in the Tokelau require further study and protection." The five species were not listed and no other details were given. Yaldwyn and Wodzicki (1979) stated that four marine turtles have been identified from local reports, and that the green turtle appears to nest but is subjected to considerable human predation. In a short interview with Mr. N. Walters at the Office for Tokelau Affairs in 1977, I was told that turtles of undetermined species nest along the ocean beach of Taulagapapa, a motu on the east side of Nukunonu (Balazs 1982a). During early 1980, correspondence pertaining to Tokelauan turtles was sent to me by the resident school principals on Nukunonu and Atafu, and the former school principal of Fakaofo now serving as the Director of Education. These letters revealed that three kinds of turtles are known to nest in Tokelau: the green turtle and, far less frequently, the hawksbill and loggerhead, Caretta caretta. The breeding season was said to extend from June through December, with the peak months being September, October, and November. Large numbers of turtles were clearly not involved, but those present were valued by the people. These facts, along with other background information contained in the letters, provided me with a sound basis for planning field research in Tokelau.

The ethnologic information on Tokelau assembled by Macgregor (1937) contains several references to sea turtles involving such aspects as fishing, cooking, ceremony, fishhooks, and folklore. Huntsman (1969) provided a description of the preparation and ceremonial distribution of two turtles captured at Nukunonu in 1967. Huntsman (1977) also recorded and translated into English the Tokelauan tale of "Hina and the turtle" which had been published earlier by Burrows (1923) in a different version.

STUDY METHODS

My study visit to Tokelau was carried out from 17 to 27 October 1981 in conjunction with a scheduled visit of the 58-m supply vessel, MV *Frysna*, chartered by the Office for Tokelau Affairs. The principal methods used to collect information on sea turtles consisted of 1) personal interviews, especially with village elders, fishermen, and other Tokelauans identified as having special knowledge; 2) firsthand surveys of beach and ocean areas at each atoll; 3) firsthand observations of the preparation and ceremonial distribution of turtles captured at Fakaofo; and 4) photographic documentation of pertinent aspects of the visit. Dossiers containing photos and drawings of the different sea turtle species were assembled for use during the interviews. These and other educational materials were left with village authorities and schools on each atoll. Many of the interviews were conducted with the aid of a translator to ensure an accurate understanding. Mr. Semu Uili, Officer for Agriculture and Fisheries, served admirably in this capacity and was of invaluable assistance as my guide and gracious host. A list of the people interviewed appears in the Appendix.

It was possible to spend 4 consecutive days and nights at Fakaofo because a general council meeting (fono) of all three atolls was held at this occasion in conjunction with the vessel's arrival. This convergence of a large number of people at Fakaofo enhanced my opportunities to gather information. The time I spent aboard the MV *Frysna* traveling between Apia and Tokelau, and back and forth between the three atolls, also afforded good opportunities to talk with people about sea turtles.

FINDINGS

Status and Ecology

Species present

The green turtle is the most common sea turtle at all three atolls of Tokelau, and is a seasonal breeder present mostly from September through November. During this time, mating pairs appear a short distance off the ocean side of the reef, and nesting occurs on certain sand beaches. For the rest of the year adults are far less frequently seen, but immature turtles about 40 to 60 cm in carapace length continue to be present in the lagoon and along the outer reef. The hawksbill is also known at all three atolls; however, Nukunonu is the only site where nesting occurs, and then only on rare occasions.[1] Most of the hawksbills seen are of an immature size that, like the young green turtles, appear to live throughout the year both in the lagoon and immediately outside the reef. The loggerhead is a third species known in Tokelau (exclusively from Nukunonu), but it is an uncommon nester. My informant from Nukunonu, 84-year-old Palehau Leone, who is an outstanding authority on all aspects of Tokelauan life, told me that "this reddish turtle comes from far away to nest, and when it does a greater number of green turtles can be expected." Vaughan (1981) mentioned a related belief at Santa Ysabel in the Solomon Islands where the capture of a loggerhead, a rare species not known to nest, is a good omen for the prospects of catching green turtles. Photographs and descriptions that I provided of the leatherback, Dermochelys coriacea, revealed that this turtle is totally unknown in Tokelau, although great interest was shown in its size, body form, and pelagic life habits.

Tokelauans call the green turtle "fonu," a general name for sea turtles also used in several other areas of Polynesia, including Samoa and Tonga. In Tahiti and Hawaii, green turtles are called "honu," and in Fiji (Melanesia), "vonu." The hawksbill in Tokelau is called "fonu una" (literally "scale turtle") because of its thick scutes. Two less common names used for this species in Tokelau are "fonu puhi" and "kea puhi," which refer to the hawksbill's beak being elongated like an eel's. Other than fonu, there is no special name for the loggerhead turtle. The name "tuahivivalu" (literally "eight backbones") was also given to me as a type of turtle. However, after considerable discussion among my informants, it was decided that this refers to an exceptionally large turtle measuring eight human hands laid along the carapace. This would be a length of at least 140 cm, the upper limit of the largest green turtles ever recorded in the scientific literature. No "tuahivivalu" are known to have been caught or seen in Tokelau during this generation. In Pukapuka the largest green turtles are called "mataweo," while the ordinary ones are "wonu" (Beaglehole and Beaglehole 1938).

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[1] Small numbers of green turtle and the hawksbill are known to nest at Olosega. The small human population is reported to take turtles and eggs from the beaches whenever possible.

A female turtle in Tokelauan is called "ika fua" and the male "ika tane." Two turtles joined together copulating are called "ulugaafonu." The word used when referring to any small or young turtle was repeatedly given to me as "kea." Similar words are used solely for the hawksbill in the Tuamotuan (tīfai-kea) and Hawaiian (honu'ea) languages of Polynesia.

Nesting habitat

The nesting habitat on all three atolls is somewhat limited by extensive shoreline areas of beachrock (limestone) and coral shingle. Fine coral sand beaches suitable for nesting are interspersed along these inhospitable shores, and probably make up not more than 25 per cent of the existing coastline on the ocean sides of the motu. Nesting is not common on the lagoon sides, even though there are some suitable sand beaches. The ocean-side beaches where nesting takes place at each atoll are shown in Figures 2 and 3. Many of these are on the east-northeast sides which are generally more windward and farthest from the motu where the villages are situated.

Most of the beaches I examined had thick vegetation growing almost to the high tide line. Nearly all of the beaches are inaccessible to nesting turtles during periods of low tide because the seaward approach over the fringing reef becomes bare and exposes jagged coral rocks. A turtle that finishes nesting at such times is completely stranded until the tide rises.

Abundance and trends

The number of adult males and females captured in recent years during each breeding season has been approximately 20 at Nukunonu, 10 at Fakaofo, and 15 at Atafu. Not much effort seems to be directed at catching the immature turtles, except on special opportunities. Based on interviews and my firsthand surveys of beaches, I estimate the number of nesting females present each season to be approximately 70 at Nukunonu, 30 at Fakaofo, and 20 at Atafu (total: 120). This initial estimate will need to be refined as more information becomes available.

I asked my elder informants to give me some idea of how many adult turtles were captured during each season when they were young men. Palehau Leone was 18 years old in 1915 and he estimated that "3-4 turtles per day" were taken at that time, or about 90-120 per season. Nemia Tuvala, 65-year-old expert fisherman of Fakaofo, recalled that at least 20 turtles were caught each season in the 1930's. Kalolo Mika, 78-year-old expert fisherman and the son of Mika, Macgregor's (1937) principal informant, stated that about 80 per season were taken at Atafu in the 1920's. This information seems consistent with Macgregor's (1937) general appraisal for Atafu in 1932 that "many turtles are caught" during the mating and nesting period.

In considering the above catch data, it is important to note that turtles can now be located and taken far more efficiently than before due to the widespread use of outboard motors and more sophisticated capture methods. Even with this increased efficiency, it is still not possible to catch as many turtles as before.

Species description

It was only possible to examine specimens of the green turtle. A male and female seen captured at Fakaofo had carapace lengths of 91 and 105 cm, respectively. I was told that females are almost always bigger than males. The shell colorations and other dorsal surfaces of the two turtles at Fakaofo differed significantly. The female was mostly black and reddish-brown with yellowish streaks. The male was basically olive and had black flecks. The plastrons of both turtles were whitish-yellow. Recently excised shells from a 103-cm female at Fakaofo, and a 104-cm female at Nukunonu, were black and olive. A 102-cm shell at the home of Luciano Perez in Nukunonu was also black and olive. Turtle shells are not commonly used for decoration in Tokelau. Instead, they are either cut up and eaten or thrown away.

At the home of Mrs. Siniua Sosene on Fakaofo, I examined a 35-cm turtle that had been raised as a pet for about 2-1/2 years. The turtle was hatched from one of four eggs she had received as part of a clutch shared among the village. The shell had radiations of reddish-brown, with cream-colored infusions and some black streaks. The plastron was whitish-yellow. This healthy, fine-looking animal was being held in a small container of sea water next to the house where it was fed fish and coconut. Every so often village children took it for a swim in the lagoon. Several turtles raised by other families from the same clutch of eggs have escaped during similar outings.

Food sources

My informants told me that the green turtle's main food source is green algae. Algae are seldom, if ever, used for human food in Tokelau, and consequently there was not a great familiarity with the species present. The hydrozoan, Velella velella (called "hehema"), was also mentioned as a food item sometimes found in the stomach of green turtles. This was reported to be a common invertebrate in Tokelau. I saw a number of them on the beach at Nukunonu, as well as aggregations floating at the sea surface as we motored through calm waters between Apia and Tokelau.

I was able to thoroughly examine the gut contents of the two turtles caught at Fakaofo. The female's digestive tract was completely empty except for a single piece of blue polyethylene plastic about 15 cm long. The male, however, had algal food material throughout its entire tract. The fresh contents of the stomach consisted mostly of the green alga, Valonia aegagropila, and lesser quantities of the brown alga, Turbinaria ornata. The only other material found was a small bird feather in the large intestine.

Epizoics and diseases

Numerous small barnacles, Platylepas hexastylos, were present on the tail and neck regions of the two adults caught at Fakaofo. In addition, the male had patches of red alga (probably Polysiphonia tsudana) growing in these same areas. The juvenile turtle being raised by Mrs. Sosene also had red alga growing on its shell.

A small number of the turtles captured in Tokelau are reported to have an abnormal condition described as "watery and shrunken flesh." Turtles with this disorder are not emaciated and cannot be recognized by any external signs. These turtles are usually not used for food, but on the rare occasions when they have been eaten, no sickness resulted. Sister Juliana, a Tokelauan serving at the Catholic Mission on Nukunonu, told me that it is traditional on her island to sing and talk in the presence of turtles that have been captured to keep their meat from becoming watery and shrunken. At times when turtles are caught late in the afternoon, it is necessary for this ritual to continue throughout the night until the next morning when butchering takes place.

The tumors or fibrous growths that are sometimes seen in Hawaiian (Balazs 1980) and other populations of green turtles are unknown in Tokelau.

Natural predators

I was unable to find any direct evidence of predation on turtles or eggs, except for human predation. Nevertheless, there are a number of species in Tokelau that constitute potential threats and undoubtedly take turtles.

In the terrestrial environment there are hermit crabs, Coenobita spp., ghost crabs, Ocypode spp., Polynesian rats, Rattus exulans, two species of frigate birds, Fregata ariel and F. minor, and reef herons, Egretta sacra. All of these are known predators of hatchlings and eggs at certain other breeding areas. Except for rats, none of the above appeared abundant at the time of my visit. However, large predator aggregations may build up at other times of the year.

In the marine environment, sharks and other carnivorous fish can prey on hatchlings, especially during the vulnerable time when they cross over a shallow reef to reach deep water. Large groupers, Epinephelus spp., sometimes prey on immature turtles up to about 30 kg, and large sharks are known to eat turtles of all sizes, including the largest adults. The tiger shark, Galeocerdo cuvier (called "mokoha"), an important predator of sea turtles throughout the tropics, occurs in Tokelau but apparently not in great numbers. At Fakaofo I saw the jaws of a 3-m tiger shark hooked earlier in the year by villagers fishing from a small boat at night just outside the reef. The stomach did not contain any remains of turtles. It was my impression that such large sharks are not common, or at least not commonly encountered, in

Tokelau. Shark attacks on humans are reported to be very rare, but this may be because Tokelauans seldom dive or swim at night.

Many people that I talked to told me of the Tokelauan belief or rumor that the mother turtle returns to the waters near her nesting site when the eggs hatch so she can eat her young. No one has actually witnessed this event or recovered hatchlings from the stomach of a turtle. Possibly such predation was indeed documented at some time in the past, since there are a few records from other areas of adult turtles (leatherbacks) eating hatchlings (ridleys).

High-seas migrations

The green turtles that breed in Tokelau are absent for most of the year. There can be little doubt that they are coming from, and returning to, some distant feeding pasture. The actual location of this resident area (or areas) is unknown, but must be many hundreds of kilometers away. Green turtles breeding at other sites in the Pacific are known to make similar migrations (see Balazs 1982b). At Scilly Atoll in French Polynesia, green turtles tagged while breeding have been recovered at foraging areas to the west all across the Pacific, including Tonga, Fiji, Wallis Island, New Caledonia, and Vanuatu.

None of my informants had ever heard of a tag being found on a turtle in Tokelau. In addition, no traditional knowledge seems to exist on where the turtles may go when they are not in Tokelau. Although admittedly speculative, I believe that a likely possibility where the turtles may go would be the coastal waters of Western Samoa. Immature and adult green turtles are found in Western Samoa, but nesting does not take place. Green turtles nesting at tiny Rose Atoll (14°33'S, 168°09'W), the geologically oldest site in the Samoan Archipelago, may also use feeding grounds in Western Samoa. However, no recoveries have thus far been made of the turtles I tagged at this site in November 1980 and October 1982.

The origin of the few loggerheads and hawksbills that nest in Tokelau is also unknown. Hawksbills could, however, be permanent residents, as is suspected for certain other areas. Loggerheads are not common in the Pacific islands, although sizable numbers occur in New Caledonia and on the Great Barrier Reef, and at least some occur in Fiji.

In considering the migrations of Tokelauan turtles, it is interesting to note that in the tale of "Hina and the turtle," Hina rides on the back of the turtle (Kea) to Fiji and Tonga, but only ventures ashore when they arrive at Vavau. I have been unable to determine if Vavau refers to the group of islands by that name in Tonga, or to Bora Bora in French Polynesia which had the ancient name of Vavau. In other Tokelauan tales, there are clear references made to the Vavau in Tonga (J. Huntsman, personal communication in April 1982).

Human Usage

Methods of capture

Most turtles captured in Tokelau are taken while they are copulating in waters just outside the reef. There is some evidence to suggest that the leeward sides of the atolls are preferred mating areas, and the lagoon waters are not usually used.

When a mating pair is sighted from land, men from the village either swim out or launch their small outboard-powered aluminum boats and cautiously approach the turtles. Using skill and strength, the turtles are physically restrained by hand or with the aid of a rope. This is essentially the same method of capture described by Macgregor (1937). In recent years, however, the use of an iron hook and line to snag turtles has become popular. Fewer turtles are lost by this technique and not as many men are needed. A hook and line also increases the chances of catching mating turtles that are accidentally encountered at night when villagers are fishing for other species. A turtle caught at Nukunonu a week before my arrival was taken under these circumstances.

A traditional belief in Tokelau is that a man whose wife is pregnant will frighten off a pair of turtles if he is involved in the attempted capture. Consequently, these men are forbidden from joining the hunting party. A woman at Fakaofo in her eighth month of pregnancy was one of several people that related this belief to me.

Another one of my informants, Hosea Kirifi, told me an interestng story about an accident that happened many years ago at Fakaofo during an attempt to catch a large turtle. One of the men became entangled in a rope he had tied to the turtle. The turtle dove and pulled the man down to a great depth. The last thing the man remembered before losing consciousness was hearing a high-pitched noise (probably from pressure against his eardrums). The other men in the hunting party thought he had surely drowned and was lost. However, a few minutes later the turtle, in a state of exhaustion, and the unconscious man still tangled in the line, rose to the surface. The man recovered and lived to an elderly age, but could never hear again.

A second method used in Tokelau to catch turtles is to find the females while they are nesting. This method is used on overnight visits to the motu to gather coconuts, or when the Council of Elders sends a special party of men to a particular motu where turtle is likely to nest. When a turtle is found nesting, it is either tied to a pole and carried or dragged upside down back to the boat.

The use of outboard motors and aluminum boats is now widespread at Fakaofo and Nukunonu and has almost completely replaced the traditional outrigger canoes made from kanava trees. In past years, these canoes were powered exclusively by sail or paddle. During my visit I only saw one such sailing canoe at Fakaofo and the few others present had outboard motors.

Greater time and effort were once required to travel to the outlying motu, some of which involve round trips of 10-22 km. Although it is now far easier to reach the motu, I was unable to determine if this has influenced the number of overnight visits being made during expeditions to gather coconuts. If fewer stays now occur because of increased mobility (e.g., the men are returning to the village to spend the night at home), then there would be less opportunity to encounter nesting turtles. However, a turtle's tracks and fresh nesting site would be found when the men return the following morning. Most of the time the eggs would be taken, and eventually the turtle if it returns to this same site to nest again.

The current ability to travel faster and easier with outboard motors does not mean that freedom exists to visit all of the motu at any time. As a traditional means of conserving the coconut resource, the Council of Elders decides which motu may be visited during a certain time period. All others are off-limits, except by special permission. This control by the Elders applies to motus owned in common by the village, as well as land held by the kāiga groups that collectively make up most of the atoll. To some extent, these restrictions have probably also served as a conservation buffer for nesting turtles.

Although seldom used, another method of catching turtles in Tokelau is to harpoon them from the reef flat at low tide when they swim in close to feed on algae. Porpoises are also occasionally taken by this technique.

The least common method of taking turtles in Tokelau is to simply find them stranded on the reef flat at low tide. Such strandings are apparently rare, or at least not often seen by the people. The two turtles captured while I was at Fakaofo were found stranded by a group of children. Nemia Tuvala of Fakaofo told me that some years ago he found an adult female stranded on the reef between Fenua Fale and Fenua Fala, the two nearly adjacent motu where the villages are located. This capture was said to be significant for the following reason. Nemia's "grandfather's grandmother" had the name of Fonu. Within this family, there is the belief that a turtle will be captured a day or two after the death of a family member. Nemia's aunt died shortly before he found the turtle. Emory (1947) reported a similar belief at Napuka in the Tuamotu Archipelago, where the spirit of a deceased person was thought to lead a turtle to land 1 year after death.

Egg collection

Clutches of turtle eggs are dug up and taken whenever they are found at Fakaofo and Nukunonu. At Atafu the Council of Elders has placed a ban on the taking of eggs, except for a few that are allowed to be removed from each nest. According to Tokelauan custom, all eggs taken at each atoll must be given to the Elders for distribution among the village. The Elders also determine when the turtle will renest by careful inspection of the opaque disk that forms on each egg and becomes progressively larger as the embryo develops. Knowing that a turtle will usually nest again at 2-week intervals, the Elders compute an estimated date for the turtle to return based on the age of the eggs from the previous clutch. Men are then sent to the motu on this date to catch the turtle when it comes ashore. The technique assumes that a turtle renests on the same motu, and this indeed happens most of the time. The same reliable method of calculating the renesting date is also used in the Solomon Islands (Vaughan 1981), Palau (Pritchard 1977), and elsewhere throughout the Pacific.

Another method used at some islands to determine the renesting date involves counting the number of eggs in the clutch. There is no known scientific basis for this practice, and it is highly unlikely that meaningful results are obtained. Johannes (1981) mentioned that this technique is used in Tokelau, when actually the literature he cited pertained to Pukapuka in the northern Cook Islands where the counting method is known to have been used (Beaglehole and Beaglehole 1938).

There is no indication in the traditional history of Tokelau that the taking of turtle eggs was ever prohibited. Macgregor (1937) does not mention turtle eggs, although he lists "birds' eggs" as one of the ancestral foods of Tokelau. Bans on the taking of turtle eggs are known to have existed within a number of other Pacific island cultures, and some are still in effect (Johannes 1978, 1981). The taking of eggs at Pukapuka was not allowed in the past (Beaglehole and Beaglehole 1938). The people of Pukapuka attribute the lifting, or cultural breakdown, of this ban as being responsible for the decline of turtles at their atoll.

The ban on taking turtle eggs at Atafu was put into effect during the early 1970's. This action appears to have resulted in part from the advice of American Peace Corps Volunteer, Alan Banner, and the South Pacific Commission's Fishery Advisor, Val Hinds. The suggestion to implement this conservation measure was probably made to all three atolls, but Atafu is the only site where it was adopted as a continuing policy.

Turtle eggs that are taken and distributed among the village may be eaten or sometimes reburied for the purpose of hatching a pet turtle. According to Kalolo Mika, turtles raised as pets in captivity are not eaten because they have an unpleasant taste. They are also not raised to a large size because of an absence of adequate holding facilities.

At Fakaofo turtle eggs are described as watery and not considered palatable if they are more than 4 days old. At Nukunonu, I was told that eggs less than 10 days old are preferred. A method of cooking turtle eggs is to roast them directly in a fire.

Ownership and restrictions

In the Tokelauan culture sea turtles along with swordfish, sailfish, porpoise, and whales,[2] are classified as "sacred fish" (ika ha). The significance of this designation is that such animals are owned collectively by the entire village, and cannot be taken for personal use. When a turtle is captured, it is ceremonially shared with everyone through an intricate and equitable procedure known as "inati." Huntsman (1969) describes the inati system as "the reflection of the Tokelauan ideology of equality, whereby each individual receives from or contributes to the village or moiety his fair share."

In past years anyone who kept a sacred fish for his own use was punished by having his house burned and his property and canoe broken up (Macgregor 1937). At the present time, a person violating this traditional code would be severely rebuked by the Council of Elders. As a result, the family would be humiliated and the stigma could last for years. I was told of an incident that happened two generations ago involving a man who caught and ate a turtle on an outlying motu. Even now this man's descendants are sometimes the subject of ridicule by other villagers as the result of this incident.

In Tokelau all of the inhabitants, including women and children, are permitted to eat turtles if they so desire. No restrictions seem to have existed in the past, although certain portions such as the head were reserved for the chief. In a number of other Pacific island cultures, turtles could formerly only be eaten by select groups, usually limited to chiefs or adult men.

Macgregor (1937) indicated that certain forms of animal life, including turtles, used to be revered as family spirits or gods. The animal so designated was never caught, injured, or eaten by members of that family. I found no evidence that this belief still exists, although certain individuals within families will not eat turtle. Possibly this involves the small number of people who have recently converted to the Seventh Day Adventist Church, some members of which will not eat turtle for religious reasons (see the Bible Leviticus 11 and 19, Deuteronomy 14).

Huntsman and Hooper (1975) mentioned that women within the Tokelauan culture are perceived as having "close links" with spirits, as well as fish, turtles, and birds. This may be the reason why no women at Fakaofo were involved in any aspect of the butchering and distribution of the two turtles I witnessed. When I inquired about this matter my informants confirmed that women are never involved, but the cultural basis for exclusion was not known.

At Atafu I was told that the green turtle and the hawksbill (though now rarely caught) are both eaten and taste equally good. The females of both species are always preferred over the males. No restrictions have ever existed on eating hawksbills, and the poisoning that occasionally happens elsewhere in the Pacific has never been known in Tokelau. However, a fatality recently resulted from eating a balloonfish (Tetraodontidae or Diodontidae) at Fakaofo, and symptoms indicative of ciguatera poisoning have occurred at Nukunonu from eating a fish called "fagamea" (probably the red snapper, *Lutjanus bohar*).

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[2] Whales are sometimes found washed up along the windward sides of the atolls.

Distribution

When a turtle or other sacred fish was caught in the old days, it was carried to the village meeting ground (malae) for ceremonial prayers of thanks offered to the god Tui Tokelau. The turtle was put on display for all to view, and later killed and cut up by a specially appointed man (tauvaega) who divided it among the people (Macgregor 1937).

Considerable ceremony and socialization are still associated with the distribution of a turtle. The tauvaega, or inati supervisor, presides over a team of men and boys that systematically divide the turtle into portions assigned to each family in the village. The entire turtle is consumed, except for the bile, scales, gut contents and, occasionally, the shell. While at Fakaofo, I was able to watch the full procedure of processing and distribution of the two turtles found stranded on the reef. The tauvaega of Fakaofo, Kalepo Mativa, as well as Nemia Tuvala and other participants, were most accommodating in allowing me full access to the work area and permission to take photographs. The following is a descriptive account of this event, starting when the turtles were first captured at about noontime on 22 October 1981.

The two turtles were transported from the reef by boat to the village motu of Fenua Fale, where they were placed on their bellies in the shade close to the lagoon shore. Although the turtles were not injured in any way, they exhibited very little activity or alertness, unlike the green turtles I am familiar with in Hawaii. They made no attempt to crawl to the water, even though it was in clear view just a few meters away. Furthermore, none of the villagers seemed concerned that they would try to escape. The only explanation I can offer for the turtles' lethargic behavior is that their earlier mating activity had left them in an exhausted state. This would be consistent with the fact that they did not swim off the reef when they sensed the tide receding, but rather allowed themselves to become stranded.

An interatoll rugby tournament was scheduled to take place that day, so after considerable discussion it was decided to postpone processing the turtles until the next morning. The turtles were eventually turned over on their backs where they remained unattended throughout the night.

Starting at about 8 p.m. and lasting until after midnight, traditional singing and dancing took place at the village meetinghouse as part of the festivities of the general council meeting. The turtles were well within hearing distance of this merriment, but not in the immediate vicinity. In keeping with the Tokelauan spirit of pride and friendly competition, people from Nukunonu later told me that turtles at their atoll are much better looked after, and never left alone, when they have to be held overnight. Ateli Perez, an elder at Nukunonu who was quoted by Huntsman (1977), provided some interesting insight on this tradition in a speech he gave at the Nukunonu meetinghouse on 10 October 1967:

> "We are all singing here in keeping with the ancient custom to which we still adhere. When a pair of turtles are captured in the late afternoon and are not used, old ladies come and guard over the turtle couple, sitting at the side and sing songs to cause them to stay awake. So we are sitting here at the side of the turtles and we sing. Because of another ancient belief, we come and sit beside the turtles lest a bush spirit (gaveve) steal them in the night. This is an ancient custom to which we still hold to this very night. This is the meaning of our joy-making and singing here."

The processing of the two turtles at Fakaofo started at about 8 a.m. A number of people, including many children, were gathered in the area. The turtles were first stunned in the traditional Tokelauan manner of delivering five to six heavy blows to the ventral neck and pectoral regions using a blunt instrument, in this case the hammer side of a long-handled axe. This causes massive internal hemorrhaging but very little external bleeding. When I first heard of this method, I was admittedly apprehensive from a humane standpoint. However, after seeing it take place, I am convinced that it is actually less cruel than many of the techniques employed elsewhere throughout the world. Sea turtles are simply not easy animals to kill or render unconscious by any method.

Immediately after striking the turtles, the plastron was removed by cutting along the border with a sharp knife. While this was still in progress, other workers were reaching into the turtle and ladling out all of the blood that had collected in the body cavity. Still other workers were busy building a number of small fires on coral stones for use as cooking stoves. Two of these sites were used to stew the blood in large metal pots.

The eggs in the female were carefully separated from the oviduct and counted into baskets woven from palm fronds. A total of 300 was present. All of them were immature and there was no sign of shelling.

After being separated from the body, the flippers, head, tail, and plastron were singed in the fires to loosen the keratinous epidermal scales. Each piece was then meticulously peeled clean of this inedible material. The four front flippers with the meaty pectoral regions still attached were each taken and presented as gifts to the visiting people from Atafu, Nukunonu, and Apia, and the general council meeting delegates.

The stomach and intestines were removed in one piece and carried a short distance into the lagoon where they were cut open lengthwise and washed clean. Along with the other viscera, this material was cut up into sections and combined with the remaining pieces of meat, bone, and cartilage.

The two shells were not cut up because they were initially intended to be saved as decoration for the village meetinghouse. This plan was later changed when offers were made to the Council of Elders to buy the shells. As a result, one was sold to a Tokelauan living in Apia, and the other to a Tokelauan residing on Fakaofo who eventually returned to New Zealand where he has lived for some years. According to Kalolo Mika, turtle shells have traditionally been cut up and eaten after removing the horny scutes. It was explained that the shell, which is mostly bone, is usually given to the young men because their teeth are strong enough to chew on it. On the other hand, the plastron, which has less bone and more cartilage and therefore is easier to chew, is given to the older people whose teeth may not be as good.

When the processing was completed, Kalepo supervised the other workers in assembling the proper allotment for each family or inati group. To serve as a guide, he had a list of the 76 family names for Fakaofo and the number of people in each unit. The quantity and composition of the shares seemed to be very carefully considered before a decision was reached. Because a sizable amount of the turtle meat had been given to the visitors, it was necessary to incorporate portions of a village-owned pig so that each share would be adequate. When the apportionment was finally completed, all of the shares rested on palm frond mats spread out neatly on the ground. A call was then given throughout the village signifying that children from each family should come to the area. After everyone had arrived, Kalepo read off each name and the children came forward with a bowl or basket to claim their share. At that time, a few immature eggs were also added by the workmen. The food was subsequently taken back to each family home where it was prepared for the afternoon meal. Methods of cooking include wrapping the meat in leaves and baking it under fire-heated rocks, or grilling the meat directly on the rocks. The stewed blood, along with small pieces of meat and viscera that had been added, were not distributed but instead eaten by the workers when their duties were finished. The entire butchering and distribution process ended at about 11:30 a.m. and took 3-1/2 hours.

The activities that I observed at Fakaofo differed in a few respects from the information supplied by Macgregor (1937) for Atafu, and by Huntsman (1969) for Nukunonu. Macgregor (1937) mentioned that the person who first sighted a turtle was entitled to claim a larger share. None of my informants indicated that this practice is followed at the present time. Huntsman (1969) stated that at Nukunonu the parts of the male and female turtles were kept separate and used in equal quantities whenever possible to make up the shares. I saw no evidence of this at Fakaofo; however, the large portions of the meat that were given as gifts may have influenced the distribution procedure. For Nukunonu, Huntsman (1969) also indicated that the head, heart, liver, and kidneys, were allocated to either the Mission personnel, the doctor, the oldest man in the village, or the workers that processed the turtle. My informants at Fakaofo told me that until recently the head was presented to the oldest man in the village as a token of respect. Although this custom was not being followed at the time of my visit, there were plans to ask the Council of Elders to have it reinstituted. According to Kalolo Mika, the head of a turtle is always given to the oldest man at Atafu. Luciano Perez explained to me that the traditional "head portion" at Nukunonu incorporates some of the neck and a nice piece of adjoining meat from the pectoral area.

Based on the shell lengths, I estimated that the total edible weight of the two turtles distributed at Fakaofo was not less than 190 kg, or 280 g (0.62 lb) for every man, woman, and child that lives on the atoll. Using the same estimate for edible weight, and the data previously presented on human population and number of turtles captured, it is possible to compute the approximate average amount of turtle consumed per person during each breeding season. The resulting values would be 1.4 kg (3.1 lb) for Fakaofo, 5.4 kg (11.9 lb) for Nukunonu, and 2.5 kg (5.5 lb) for Atafu. These quantities make a distinct contribution to the protein nutrition of the Tokelauans. However, to be accurately appraised, the values must also be viewed in light of the enjoyment that is derived from eating this highly prized and savory food.

Other cultural aspects

During the course of my visit to Tokelau, and my literature search, a number of miscellaneous cultural components involving sea turtles were identified.

The school principal at Atafu, Tenise Atoni, told me that the uneaten bone scraps from the shares received by each family are usually thrown into the ocean in the belief that they will attract turtles to the atoll. In Hawaii the opposite view is held, at least for raw turtle parts and blood, and discarding such material into the sea is believed to drive turtles away.

There is a Tokelauan expression called "hila fonu" for a particular red sunset. Hosea Kirifi told me that when a hila fonu is observed a turtle is likely to come ashore in the evening. Macgregor (1937) also mentioned this expression, which he wrote as "la sila fonu" and translated as "the sun like a turtle's breastplate." This was listed as a descriptive Tokelauan phrase for an "orange reflection of the sunset in the clouds, common near the equator."

Macgregor (1937) stated that in the old days the ear lobes of all babies were perforated shortly after birth, and that earrings of turtle shells or bone were sometimes inserted later in life. Although a number of people that I encountered had a pierced ear, none of them had this type of earring. Macgregor (1937) also described the ancient use of turtle bones made into tattoo puncturing instruments (pakiau) and thatching awls for splitting pandanus leaves. I found no indication of these items being currently used. Tattooing is reported to have been banned when the missionaries first arrived.

Throughout the Pacific islands the thick horny scutes from the shell of the hawksbill turtle were formerly a premium material for making fishhooks. Two types were crafted in Tokelau: the one-piece hook used for line fishing with bait, and the composite hook used for trolling from a canoe or casting from shore (Macgregor 1937). Iron hooks and plastic lures have now replaced these traditional products, mostly because they are convenient to obtain, but also due to the present scarcity of adult hawksbills. I did, however, learn of a possible renewed interest in making the traditional hooks and teaching this skill to the younger generation. In this regard, I was even asked if I knew of a source where hawksbill scutes could be bought for such a purpose.

Tokelauan handicrafts are recognized as being among the finest in the Pacific islands. The most commonly produced items are woven baskets, fans and mats, and small boxes with tightly fitting lids carved from kanava wood. Two other crafted items also of superb quality, but less commonly seen, are carved wooden turtles and authentic-looking turtle shells. The shell replicas are usually made from *Tournefortia* ("tausunu") wood. Iere Kirifi of Fakaofo is a master woodcarver of these fine objects.

Since the willing conversion of the people to Christianity, there has been no form of worship to the ancient god Tui Tokelau, even though a portion of this coral-rock image is still present in the meetinghouse at Fakaofo. An invocation said to Tui Tokelau in the old days asked that the heavens send down the necessities of life to their small atolls--rain, calm, light, coconut blossoms, fish, and among other things, "he tai fonu" (plenty of turtle).

Singing and dancing continue to be an integral part of the Tokelauan culture. One of the traditional songs for dancing that Macgregor (1937) recorded from Kalolo Mika's father in 1932 tells of a turtle hunt in which Tinilau, a mischievous character of Polynesian mythology, allows the turtle to escape. The title of this short composition is "Song of catching the turtle," and the translated words are as follows:

"The turtle of the deep sea,
The turtle of the deep sea is hunted.
Chase away the young children.
Who congratulates Tinilau
Alas! there is nothing.
Tinilau continues to dance."

RECOMMENDATIONS FOR CONSERVATION

The information brought together in this paper should give the Tokelauans a better perspective of the nature and limits of their sea turtle resource. As the first document of its kind dealing with the turtles of Tokelau, the report should also be a stimulus for discussions within the Council of Elders at each atoll. I am hopeful that this increased awareness and focus of attention will result in steps to strengthen the survival outlook of turtles and their traditional role in the Tokelauan culture.

The available evidence strongly suggests that there has been a long-term decline in the number of turtles breeding in Tokelau. There has also probably been a reduction in the size of the adults, considering that much larger turtles (tuahivivalu) are known to have existed in past years. The most probable major cause of this deterioration is the biological inability of the turtle stock to remain stable against the levels of harvesting of adults and eggs that have been carried out over the years. Although these excessive harvesting levels may be partially caused by hunting pressures at the distant (and unknown) feeding areas, it is likely that the greatest impacts result from catching too many turtles and digging up too many eggs in Tokelau where breeding occurs. All sea turtles are known to be particularly vulnerable at their breeding site. This is because the reproductively mature and ecologically more valuable adults converge at relatively small areas where they are more susceptible to capture due to their density, high visibility, preoccupation with mating, and excursions on land to nest. When these same adults are at their distant feeding areas, they are usually distributed over many miles of coastal waters, are not readily visible, and almost never go ashore. In the feeding areas they are simply much more difficult to find and catch.

In the past, the mechanisms used by certain Pacific islanders to protect turtle stocks from overharvesting included prohibitions on taking eggs or taking adults while they are on the beach, establishing certain motu as inviolate sanctuaries, permitting only a certain number of turtles to be captured, and restricting the consumption of turtles to chiefs. None of these practices seem to have existed in Tokelau, although possibly at one time there was a total ban on taking eggs, such as the one known at the closest neighboring atoll to the east, Pukapuka. Even without such a ban, I suspect that turtles in Tokelau were fairly well buffered during the old days because of the greater difficulties in traveling to the outlying motu and outside the reef to catch them. Also, a greater percentage of the turtles pursued may have evaded capture in the past when the iron hook-and-line technique was not employed, and outboard motors were not available. The fact that special rules governing the taking of turtles apparently were not imposed in Tokelau suggests to me that a very large supply of turtles may have existed in relation to the human population. If this was true, as it may very well have been, the governing elders and chiefs would not have felt any need to limit the number of turtles captured. In the resource-limited atoll environment of Tokelau, the appearance of large numbers of turtles at a certain time of the year, and their departure just a few months later, could understandably motivate the small human population to catch as many as their hunting capabilities and rate of consumption would allow. Under these fruitful conditions, which undoubtedly continued year after year with little perceptible change, there would have been no reason to believe that this particular resource actually did have limits. McCoy (1974) described such a philosophy in the Caroline Islands where the seasonal coming and going of breeding turtles have falsely engendered "a faith in their perpetual return."

Whereas fewer turtles now nest in Tokelau, they have by no means vanished altogether. However, if the downward trends continue, this unfortunate outcome could very well take place. There are a number of examples of this pattern at other Pacific islands to support such a prediction. Because of our present inadequate understanding of the population dynamics and life history of sea turtles, there are no proven or guaranteed methods for rebuilding a depleted stock. Nevertheless, there are a number of conservation practices that can reasonably be expected to aid in the restoration. Green turtles living in the wild may take many years, even decades, to grow to maturity, so the implementation of these practices cannot be expected to produce quick results. Instead, any sacrifices made by this generation of Tokelauans, by taking fewer turtles and foregoing egg collection, must be regarded as an investment to benefit their grandchildren and subsequent generations. This may be a difficult challenge for people living in a remote atoll environment. However, some action is essential if the turtle resource in Tokelau is to be sustained. From information I received during my visit, it would appear that the survival problems confronting turtles are similar to the difficulties being experienced by the kanava tree, which also takes many years to reach a large size. I therefore believe it is necessary for Tokelauans to consider turtles from the same judicious perspective as they now view the kanava tree. Both of these components of the environment require special management and planning for the future.

In conclusion, I will offer a list of conservation recommendations for the Council of Elders to consider at each atoll. In this list I have purposely only presented a basic framework. If the decision is made to adopt some of these measures, which I hope it will be, then the details must of course be worked out by the Elders themselves to ensure compatibilty with Tokelauan ideals and way of life. My suggested conservation measures or options to aid sea turtles in Tokelau are as follows:

1. The collection of eggs should be stopped at all three atolls. Eggs should be left in their nests on the beaches to incubate naturally and produce hatchlings that can replenish the turtle stock. Atafu has already initiated such a measure, and the other two atolls should follow this example. The collection of one or two egg clutches each season under the Elders' supervision would be appropriate to meet the needs of villagers who want to raise a few turtles for pets.

2. All hawksbill and loggerhead turtles should be granted full protection for at last 10 years in an effort to prevent these species from becoming extinct as a breeding stock in Tokelau.

3. At each atoll, some limit or quota should be placed on the number of green turtles that are captured. Currently, there are no limits and as many as possible are taken. Consideration should be given to taking more males than females, since each male is capable of fertilizing several females. In setting quotas, as many females as possible should be permitted to escape capture so they can lay eggs to replenish the stock. The females that are allowed to be taken should be captured later in the breeding season (November and December) after they have had the chance to lay eggs.

4. Any female taken on the beach should be allowed to first nest and lay her eggs.

5. Certain motu, or defined sections of known nesting beach at each atoll, should be designated as "turtle sanctuaries" for the purpose of replenishing the stock. No turtles or eggs should be taken from these sites.

6. The use of more efficient and so-called modern methods of catching turtles in the water should be discouraged. The traditional manner of catching turtles should be encouraged because it involves challenge, strength, skill, pride, and a sense of accomplishment.

7. Tokelauan sea turtles or their parts should not be sold for money. The turtles are simply too valuable of a resource to the culture. The selling of such a native resource, once started, is difficult to stop and is a proven social and ecological disruption.

8. The schools should include information in their teaching program that covers the interesting cultural, biological, and conservation aspects of sea turtles. The teaching program should especially focus on young children.

9. A special effort should be made to strengthen or restore any appropriate cultural aspect that involves sea turtles (i.e., songs, dances, folklore).

10. Consideration should be given to teaching the young people the skill of making traditional fishhooks for fishing purposes from the scutes of the hawksbill turtle. An ample quantity of the raw scutes needed for this purpose can probably be obtained at no cost from confiscated stock being held by U.S. Government officials in Hawaii. Under no circumstances should hawksbill scutes be bought from a commercial source, since this species is seriously endangered with extinction throughout most of its range.

11. Records should be kept of the shell length, sex, capture location, and number of turtles taken during each season. Also, if interest exists, tags should be used at each atoll to try to find out where the turtles go when they are not in Tokelau.

ACKNOWLEDGMENTS

I would like to express my sincere gratitude to the Council of Elders, the Faipule, and the Pulenuku of Fakaofo, Nukunonu, and Atafu for allowing me to visit their atolls to undertake this field study. I am also particularly grateful to Hosea Kirifi who originally encouraged me to pursue this work, and to John Larkindale, Official Secretary of the Office for Tokelau Affairs, for endorsing my research proposal and coordinating all aspects of the trip. Along with the people listed in the Appendix, everyone that I met in Tokelau displayed warm hospitality and made special efforts to answer my many questions. I am appreciative of their interest and assistance. As previously mentioned, Semu Uili was my principal translator, guide, and host. I want to thank Semu and his family for their help. Without Semu's direct involvement, it would not have been possible to achieve my objectives within the limited time available.

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Appendix: Persons interviewed in Tokelau

Nukunonu

Palehau Leone - 84-year-old Elder
Lucianno Perez - Fisherman and Principal of Matiti School
Henry Joseph - Fisherman and Tokelau Public Service
Sister Juliana Perez Soln - Catholic Mission
Niko Pule - Fisherman
Kalolo Perez - Tokelau Public Service

Atafu

Kalolo Mika - 78-year-old Master Fisherman and son of Mika, Macgregor's (1937) principal informant
Amusia Patea - Faipule
Tema Nouata - Pulenuku
Tenise Atoni - Principal of Matauala School
Aleni Viliamu - Tokelau Public Service

Fakaofo

Nemia Tuvala - 65-year-old Master Fisherman
Kalepo Mativa - Tauvaega
Hosea Kirifi - Tokelau Director of Education
Siniua Sosene - Owner of captive-reared turtle
Elizabeth and John Pereira - Fisherman and resident
Moana Rimoni - Resident
Mr. and Mrs. Fetalaiga Uili - Fisherman and resident
Senitu Iasona - Participant in inati ceremony
Sakaria Petelesio - Tokelau Public Service
Janeta Siaon - Resident

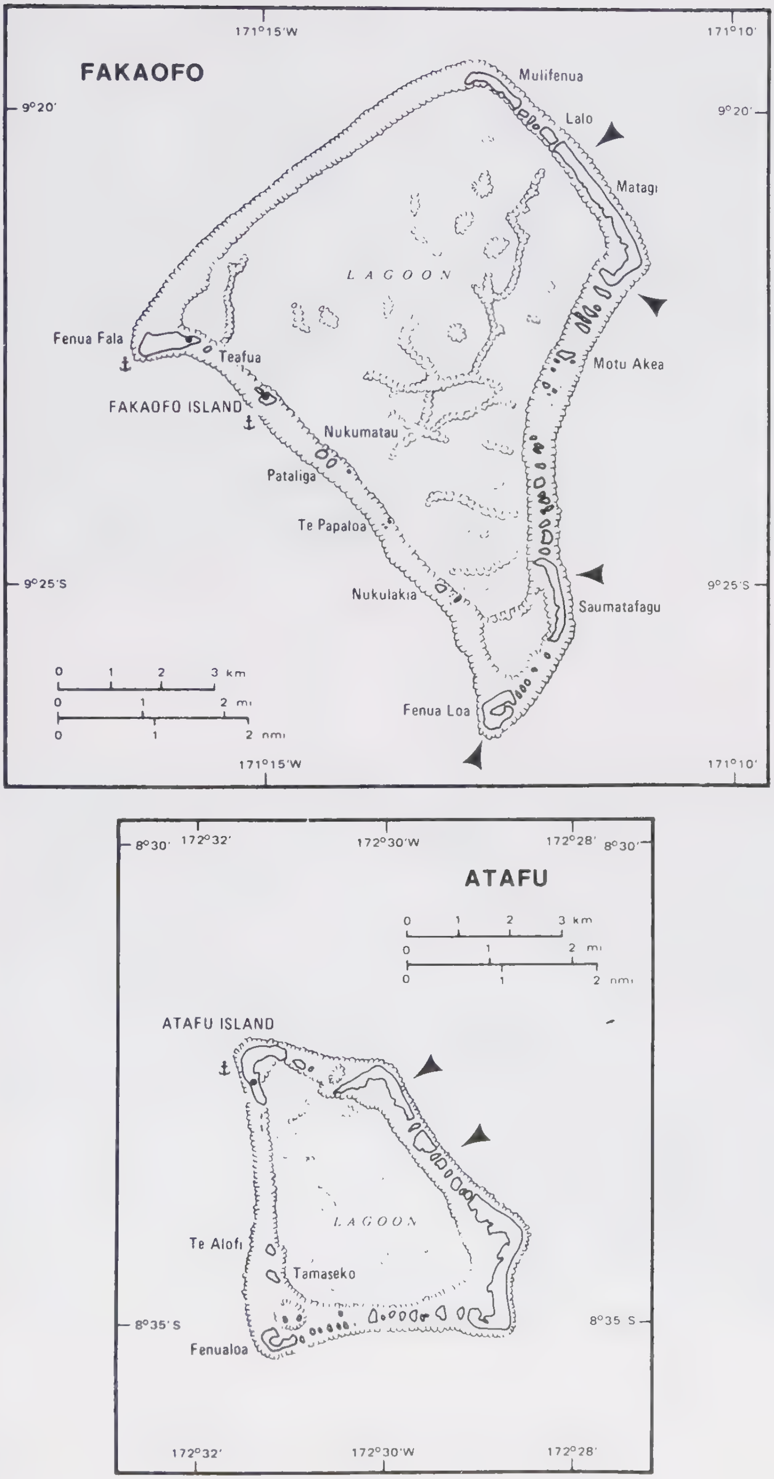


Fig. 2. Principal nesting areas at Atafu and Fakaofo

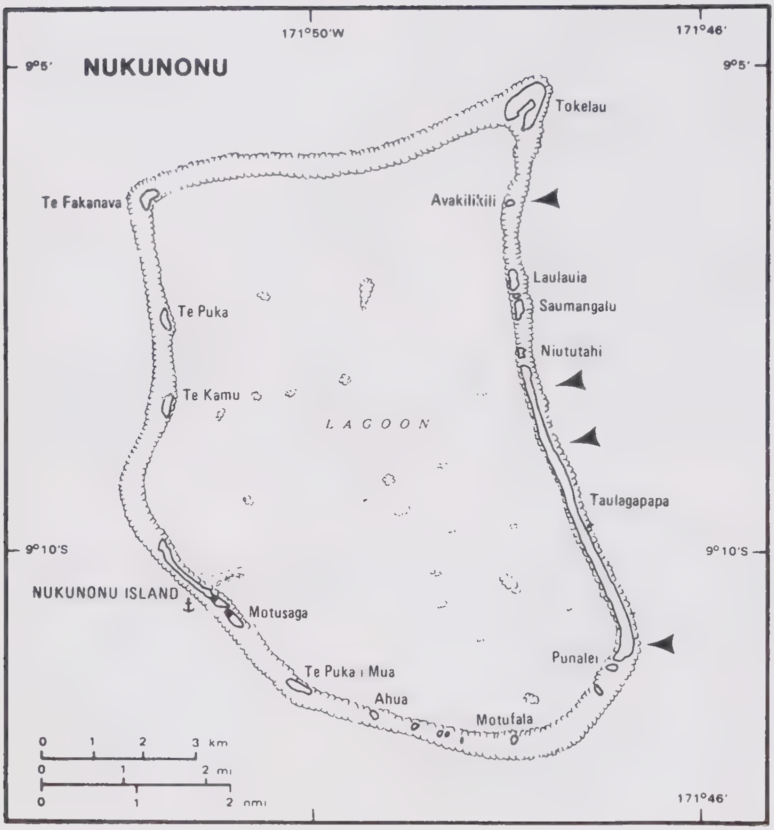
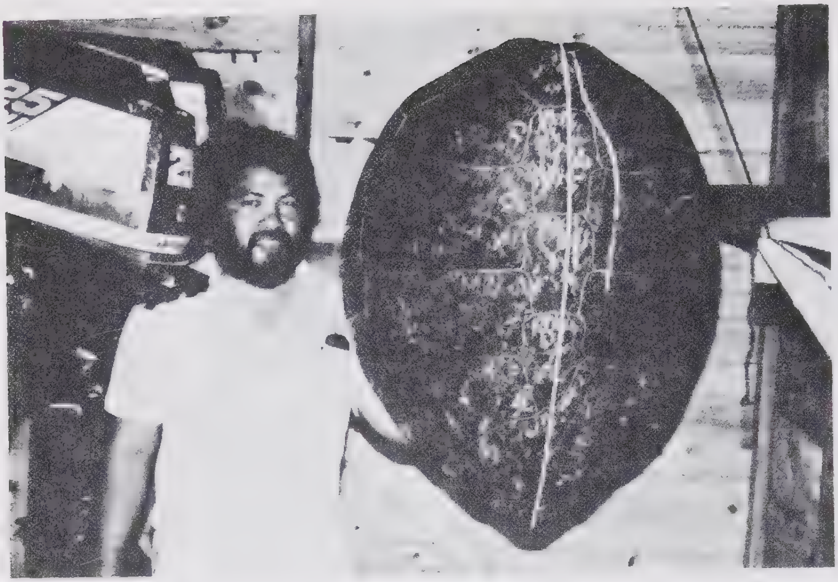


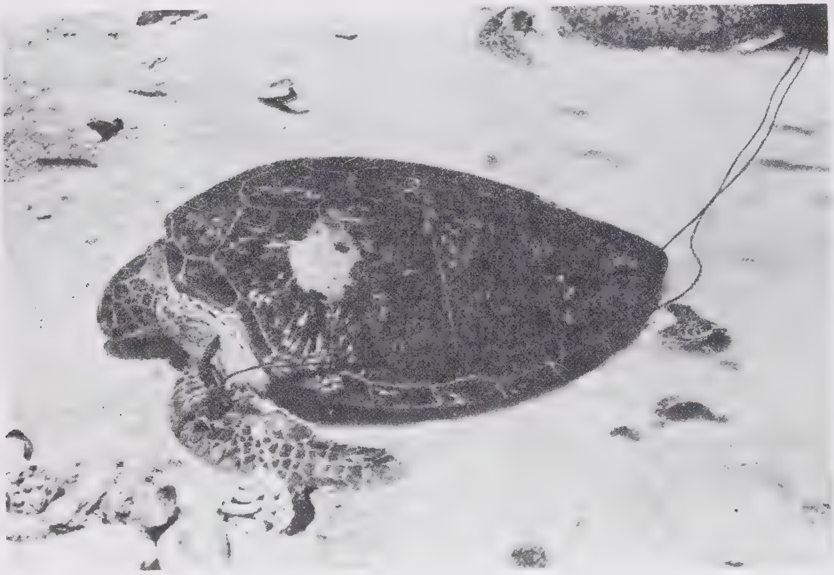
Fig. 3. Principal nesting areas at Nukunonu

1. Nesting beach at Nukunonu at low tide

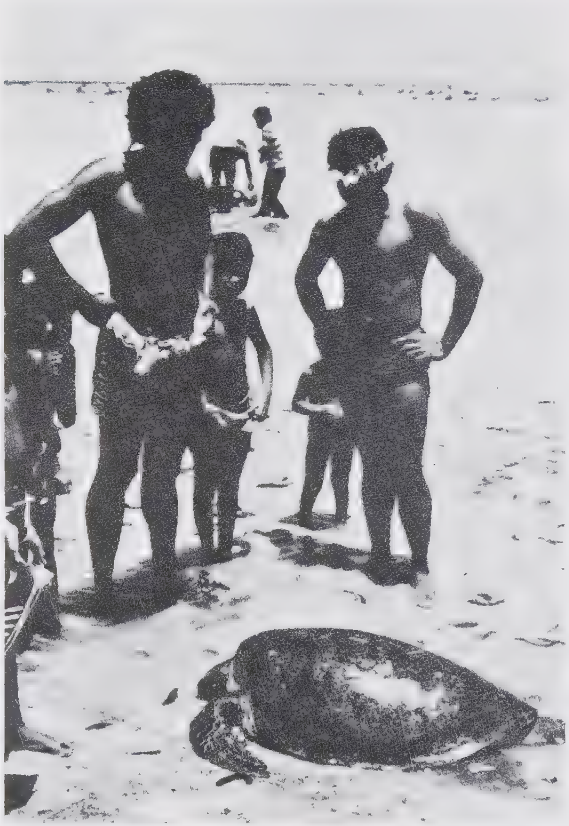
2. Ocean shoreline at Atafu showing jagged coral rock and wrecked Taiwan fishing vessel



3. Henry Joseph with the 104-cm carapace of a green turtle caught at Nukunonu



4. Adult female green turtle caught while stranded on the reef at Fakaofo



5. Adult male green turtle caught at Fakaofo

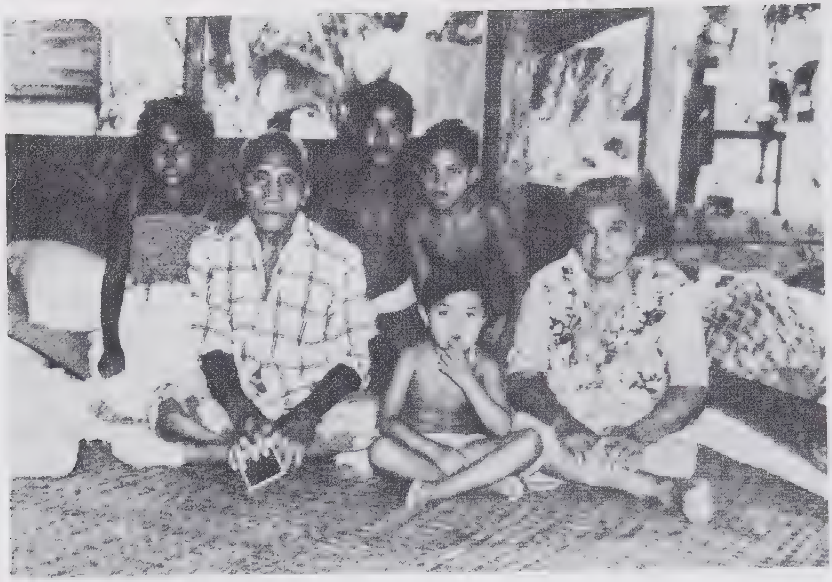
6. Siniua Sosene at Fakaofo with her captive-reared pet green turtle

7. Kalepo Mativa, the tauvaega of Fakaofo, presiding over the distribution of turtle

8. Village children at Fakaofo after receiving their family share of turtle meat and immature eggs

9. Village landing and small boat channel at Fenua Fale, Fakaofo; the MV Frysna is offshore

10. Village landing at Nukunonu



11. Master Fisherman Kalolo Mika and relatives in their family home at Atafu

12. Fleet of aluminum boats with outboard motors anchored off Fenua Fala at Fakaofo

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SUMMARY PAPER

Reduction of Bias Generated by Age-Frequency Estimation Using the von Bertalanffy Growth Equation[1]

NORMAN V. BARTOO[2] and KEITH R. PARKER[3]

INTRODUCTION

Complex population dynamics techniques rely heavily on age structure information. For some species, accurate ageing methods have not been developed. Often the age structure of a fisheries catch (age-frequency) is estimated from sampled length-frequency (Majkowski and Hampton 1983), the age relationship being described by either an age-length key or a growth curve, such as the von Bertalanffy growth curve (Ricker 1958). The growth curve method is used when there are insufficient data to construct an age-length key. But as noted by Kimura (1977) and later demonstrated by Westrheim and Ricker (1978), under conditions of varying year-class strength and substantial overlap of lengths between ages, age-length keys can yield nearly useless estimates of numbers-at-age. Even with bias correction procedures, the construction of a sufficient key can present difficulties.

In this paper we deal specifically with the von Bertalanffy growth equation and the application of stochastic methods to reduce or eliminate biases. However, it should be noted that the method presented here may be applied to any growth equation, as well as to cases where no growth equation has been fitted or where growth is discontinuous, as in crustaceans.

The von Bertalanffy growth equation mathematically models the relationship between age and length, length being the dependent variable (see Equation (1)). As suggested by Gulland (1969), age can be estimated from length by algebraically rearranging the growth equation so that age is the dependent variable (see Equation (2)). Regardless of whether length or age is the dependent variable, the von Bertalanffy relationship is deterministic, i.e., there is a one-to-one correspondence between age and length.

Use of the von Bertalanffy growth equation for age-frequency estimation results in several types of biases (Powers 1983), different from those inherent in age-length keys. In this paper we document these biases and propose a method for their resolution.

AGE-FREQUENCY BIASES

When growth is modeled according to the von Bertalanffy age-length relationship (Brody 1945; Ricker 1958)

$$L_t = L_\infty \text{ (1-exp } [-k(t-t_0)]), \qquad (1)$$

then age, t, can be converted to length:

$$t = t_0 + \ln (1 - L_t/L_\infty)/(-k) \qquad (2)$$

where L_t = length at age t
L_∞ = the asymptotic length
k = the rate at which length reaches L_∞, and
t_0 = hypothetical age at which fish would have zero length.

When computing numbers-at-age from Equation (2), estimation bias occurs from several sources. One bias is due to L_∞ being a fitted parameter. Thus, all numbers-at-length greater than L_∞ must either be eliminated or arbitrarily distributed to older ages. Bias also results when lengths approach L_∞ and are mathematically allocated to ages above those attainable by fish within the stock. As lengths (L) approach L_∞, Equation (2) will yield unreasonably old ages (i.e., ages greater than are known to occur).

Additional bias results from the deterministic nature of the von Bertalanffy equation. For example, back calculations of length to age from Equation (2), which are on a one-to-one basis, result in one determined age for any length. In reality, there can be a number of possible ages for any given length, the most probable age-at-length being that with the highest relative contribution of numbers-at-length. Since these back calculations are without probabilistic arguments, the determined age is not necessarily the most probable for the given length.

Back calculations of length to age also result in a mathematical estimation bias due to the substitution of independent and dependent variables in moving from Equation (1) to Equation (2). The degree of bias is likely to be a function of the amount of residual error in estimating length at age in fitting Equation (1). The bias will probably not be consistent between cases and the degree of bias will have to be considered separately for each case. Consequently, biases associated with equation transformation are not specifically dealt with here.

A computer model can demonstrate these biases. For von Bertalanffy parameters L_∞ = 90.0 units, t_0 = 0.0 units, and k = 0.30, predetermined numbers-at-age are assumed normally distributed with a standard deviation equal to 3 units about the von Bertalanffy length-at-age Equation (1), for ages (1) through (10). A length-frequency vector is then generated by: 1) Multiplying the number-at-age times the probability of age occurring within each 0.5 unit length interval, thus generating a vector of

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[1] This paper is summarized from research conducted by the authors and appears in *Fishery Bulletin*, Vol. 81, No. 1, p. 91-96.

[2] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038.

[3] 1837 Puterbaugh Street, San Diego, CA 92103.

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number-at-length for length intervals between 0 and 100 units for each age, and 2) accumulating numbers-at-length for each length interval over all ages. The numbers-at-age are then deterministically estimated from Equation (2) by accumulating numbers-at-length over the length intervals at age.

The bias from this model is illustrated by input and back-calculated numbers-at-age and their differences, which are listed in columns 2, 3, and 4, respectively, of Table 1. The input numbers-at-age represent a sample age distribution with varying year-class strengths. The differences in column 4 indicate a strong bias which increases with overlap of length distributions at age. The estimated ages of 111 fish were greater than the maximum age, 10. Thirty-five had lengths greater than L_∞ and, consequently, were not classifiable.

Table 1.—Input and estimated numbers-at-age for both the deterministic (column 3) and stochastic (column 5) models, with the input numbers-at-age in column 1. The difference between the input numbers-at-age and the deterministic estimates are given in column 4.

Estimated	Numbers at age			
Age (1)	Input (2)	Deterministic (3)	Diff. (4)	Stochastic (5)
1	200	199	1	200
2	400	399	1	400
3	800	760	40	800
4	200	267	−67	200
5	600	441	159	600
6	300	378	−78	300
7	400	320	80	400
8	300	258	42	300
9	100	164	−64	100
10	100	68	32	100
>10	—	111	−111	—
Inf.	—	35	−35	—

STOCHASTIC MODEL

With estimated variance of length-at-age, a stochastic model can be built from the von Bertalanffy relationship (or any other growth relation): For any age the probability of a specified length interval is the probability of that interval taken over all length intervals containing that age. Thus, for all ages, a probability matrix ("P"-matrix) of dimension r by c can be computed, where r = the number of rows, or length intervals, and c = the number of columns, or ages, then $P(1,1) = P$ (max. length, min. age). If the number-at-age vector is "a" ($a_{(1)} = a$ (min. age)) and the number-at-length vector is L ($L_{(1)} = L$ (max. length)), then

$$P\,a = L. \tag{3}$$

And as long as $r > c$, then the numbers-at-age vector can be uniquely solved via least-squares:

$$a = (P'P)^{-1}P'L. \tag{4}$$

Applying this stochastic method (Equation (4)) to the previous example, the numbers-at-age generated from the number-at-length vector is given in column 5 of Table 1. Since the probabilities of the P-matrix are the same as those used to generate the number-at-length vector, it is not surprising that the solution yields unbiased results. This computed example illustrates that the stochastic method yields unbiased estimates of age-frequency.

DISCUSSION

Calculation of age from length via the von Bertalanffy growth equation results in several types of bias. The degree of bias is proportional to overlap in lengths-at-age and changes with weak or strong year-classes. When overlap increases with age, age-frequency estimates will generally be more biased for older ages than for younger ages. When overlap occurs, biases will always result, since the numbers-at-length will be allocated to unreasonably old ages. Any numbers-at-length for lengths greater than L_∞ will be undetermined in age estimation, resulting in downward biases for those ages contributing such lengths.

Age estimation biases can be effectively removed by creating a stochastic model based on a matrix of length interval probabilities at age. The probability matrix (P-matrix) is independent of year-class strength and will effectively remove all sources of estimation bias, except that due to random variation in length-frequency estimation. A probability model of the distribution of length-at-age with estimated parameters is necessary for estimating probabilities of length intervals at age for the P-matrix. As long as the von Bertalanffy growth parameters are correct, the stochastic method based on accurate estimates of variance in length-at-age will yield unbiased results.

There may be serious implications to the bias introduced by using the von Bertalanffy equation without bias correction. In fishery management, the overestimation of maximum age by the deterministic von Bertalanffy equation may produce underestimates of mortality rates, which may result in overestimates of population size and recruitment. Further, the deterministic method tends to "fill in" weak year-classes, which results in underestimates of year-class variability and overestimates of recruitment stability. In general, all of these affect accuracy of a stock assessment and contribute to improper advice for fishery management.

Application of the stochastic method shown here to cover other growth equations and situations, such as discontinuous growth, is handled by simply estimating appropriate elements in the P-matrix for each case.

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STOCHASTIC AGE-FREQUENCY ESTIMATION USING THE VON BERTALANFFY GROWTH EQUATION

NORMAN W. BARTOO[1] AND KEITH R. PARKER[2]

ABSTRACT

The method of estimating age frequency from length frequency via the von Bertalanffy growth equation is deterministic and yields biased results. Most of the bias can be removed by incorporating a stochastic element in the von Bertalanffy relationship. The stochastic element is based on estimated probabilities of lengths by intervals at age, the probabilities being estimated from variances in lengths-at-age. Based on age-length samples from the Pacific bonito fishery the stochastic method gives improved age-frequency estimates over those obtained by the deterministic method. The stochastic application may be generalized to all growth models including discontinuous growth such as in crustaceans.

Complex population dynamics techniques rely heavily on age-structure information. Frequently, appropriate assessment techniques for a stock require an estimate of the age frequency of that stock. For example yield-per-recruit analysis (Ricker 1958) is computed on the dynamic relationship between growth and mortality: Mortality rates when computed via cohort analysis (Murphy 1965) are based on estimated age frequency.

For some species accurate aging methods are not available. When feasible, determining the age of fish and consequently computing an age frequency are most accurately accomplished by visual inspection of scales, otoliths, or other structures (Ricker 1958). Such visual inspection is time consuming and often expensive. To reduce the cost and time of estimating the age structure of a fisheries catch, age frequency is usually estimated from sampled length frequency, the age-length relationship being described by either an age-length key or a growth curve such as the von Bertalanffy growth curve (Ricker 1958). The growth curve method is used when there are insufficient data to construct an age-length key.

Age-length keys work on the principle that age can be estimated from length using information contained in a previously or concurrently aged sample from the population. As long as the proportion of length-at-age remains the same for all ages, then the age-length key will yield unbiased estimates of age for any sampled lengths from that population. However, since the estimated parameters of an age-length key—proportions of age-at-length—are dependent on the sampled population used to construct the key, the application of the key to the population with altered age structures can yield inaccurate results. Kimura (1977) and later Westrheim and Ricker (1978) demonstrated that under conditions of varying year-class strength and substantial overlap of lengths between ages, age-length keys can yield nearly useless estimates of numbers-at-age.

Clark (1981) effectively removes age-length key bias by first proportioning numbers in length intervals at age over time and then using the matrix of these proportions standardized over time to compute least-squares estimates of age frequency from the vector of length frequency. Effective applications of many stock assessment growth and mortality based methods require that ages are expressed in fractions of years (Ricker 1958; Lenarz et al. 1974). The large number of aged fish required to construct a sufficient key for a large number of ages is difficult and expensive to attain. Even with Clark's bias correction procedure, the construction of a sufficient key can present difficulties due to data needs.

In this paper we deal specifically with the von Bertalanffy growth equation and the application of stochastic methods to reduce or eliminate biases. However, it should be noted that the method presented here may be applied to any growth equation as well as to cases where no growth equation has been fitted or where growth is discontinuous as in crustaceans.

The von Bertalanffy growth equation mathe-

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[1] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038.

[2] 1837 Puterbaugh Street, San Diego, CA 92103.

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matically models the relationship between age and length, length being the dependent variable (see Equation (1)). As suggested by Gulland (1973), age is estimated from length by algebraically rearranging the growth equation so that age is the dependent variable (see Equation (2)). Regardless of whether length or age is the dependent variable, the von Bertalanffy relationship is deterministic: There is a one-to-one correspondence between age and length.

For the von Bertalanffy growth equation, age frequency is estimated from a length sample as follows:

1) For each length compute the corresponding age.
2) For each age interval, usually the interval between midpoint ages of adjacent ages, sum the number of aged fish falling within the interval.
3) The age frequency is then the total number of aged fish falling within each age interval.

Use of the von Bertalanffy growth equation for age-frequency estimation results in several types of biases, different from those inherent in age-length keys. This paper documents these biases and proposes a method for their resolution.

BIASES

When growth is modeled according to the von Bertalanffy age-length relationship (Brody 1945; Ricker 1958),

$$L_t = L_\infty \ (1 - \exp[-k(t - t_0)]), \qquad (1)$$

then age, t, can be converted to length:

$$t = t_0 + \ln \ (1 - L_t/L_\infty)/(-k) \qquad (2)$$

where L_t = length at age t
L_∞ = the asymptotic length
k = the rate at which length reaches L
t_0 = hypothetical age at which fish would have zero length.

When computing numbers-at-age from Equation (2), estimation bias occurs. One bias is due to L_∞ being a fitted parameter. Thus, all numbers-at-length greater than L_∞ must either be eliminated or arbitrarily distributed to older ages. Bias also results when lengths approach L_∞ and are mathematically allocated to ages above those attainable by fish within the stock. As lengths (L) approach L_∞, Equation (2) will yield unreasonably old ages.

Additional bias results from the deterministic nature of the von Bertalanffy equation: Back calculations of length to age, Equation (2), are on a one-to-one basis. Thus, for any length there is a determined age. In reality, there can be a number of possible ages for any given length, the most probable age-at-length being that with the highest relative contribution of numbers-at-length. Since these back calculations are without probabilistic arguments, the determined age is not necessarily the most probable for the given length.

Back calculations of length to age also result in a mathematical estimation bias due to the switching of independent and dependent variables in going from Equation (1) to Equation (2). The degree of bias is likely to be a function of the amount of residual error in fitting Equation (1). The bias will probably not be consistent between cases and the degree of bias will have to be considered separately for each case. Consequently this bias is not specifically dealt with in this paper.

A computer model can readily demonstrate this bias. For von Bertalanffy parameters: L_∞ = 90.0 units, $t_0 = 0.0$ units, and $k = 0.30$, predetermined numbers-at-age are arbitrarily distributed normally with a standard deviation equal to 3 units about the von Bertalanffy length-at-age, Equation (1), for ages I through X. A length-frequency vector is then generated by 1) multiplying the number-at-age times the probability of age occurring within each 0.5 unit length interval, thus for each age generating a vector of number-at-length for length intervals between 0 and 100 units, and 2) accumulating numbers-at-length for each length interval over all ages. The numbers-at-age are then deterministically estimated from Equation (2) by accumulating numbers-at-length over the length intervals at age.

The bias from this model is illustrated in Table 1. Input and back-calculated numbers-at-age and their differences are listed in columns 2, 3, and 4, respectively. The input numbers-at-age represent a sample age distribution where either catchability, recruitment, mortality, or some combination thereof, are age-class variant. Differences, column 4, indicate a strong bias which increases with overlap of length distributions at age. One hundred and eleven fish were aged to be

TABLE 1.—Input and estimated numbers-at-age for both the deterministic (col. 3) and stochastic (col. 5) models, with the input numbers-at-age in column 2. The differences between the input numbers-at-age and the deterministic estimates are given in column 4.

Age (1)	Numbers-at-age Input (2)	Deterministic (3)	Difference (4)	Stochastic (5)
I	200	199	1	200
II	400	399	1	400
III	800	760	40	800
IV	200	267	−67	200
V	600	441	159	600
VI	300	378	−78	300
VII	400	320	80	400
VIII	300	258	42	300
IX	100	164	−64	100
X	100	68	32	100
>X	—	111	−111	—
Inf.	—	35	−35	—

greater than the maximum age, 10. Thirty-five had lengths greater than L_∞ and, consequently, were not classifiable.

BIAS RESOLUTION

With estimated variance of length-at-age a stochastic model can be built from the von Bertalanffy relationship: For any age the probability of a specific length interval is the probability of that interval taken over all length intervals containing that age. Thus for all ages a probability matrix ("P"-matrix) of dimension r by c can be computed, where r = the number of rows, or length intervals, and c = the number of columns, or ages, then $P(1,1)$ = (max. length, min. age). If the number-at-age vector is "a" (a_1 = (min. age)) and the number-at-length vector is L (L_1 = (max. length)), then

$$P\,a = L. \tag{3}$$

And as long as $r > c$ then the numbers-at-age vector can be uniquely solved via least-squares:

$$a = (P'P)^{-1}P'L. \tag{4}$$

Applying this stochastic method (Equation (4)) to the previous example, the numbers-at-age generated from the number-at-length vector are given in column 5 of Table 1. Since the probabilities of the P-matrix are the same as those used to generate the number-at-length vector, it is not surprising that the solution yields unbiased results. This computed example illustrates that the stochastic method yields unbiased estimates of age frequency.

PACIFIC BONITO

For the Pacific bonito, *Sarda chiliensis*, of the eastern tropical Pacific, Campbell and Collins (1975), using ages determined from otoliths, estimated the von Bertalanffy growth parameters to be $L_\infty = 76.87$ cm, $t_0 = -0.785$ yr, and $k = 0.6215$. Numbers-at-length for 1 cm intervals for ages I through V are shown in Figure 1 with the corresponding length-frequency plot in Figure 2. These numbers represent the 1973 catch from California waters and are a subset of the data used to estimate the von Bertalanffy parameters. This example serves to demonstrate bias and illustrate application of the stochastic method. If desired a variance-covariance matrix can be generated (Draper and Smith 1981) to estimate precision in the resulting age structure.

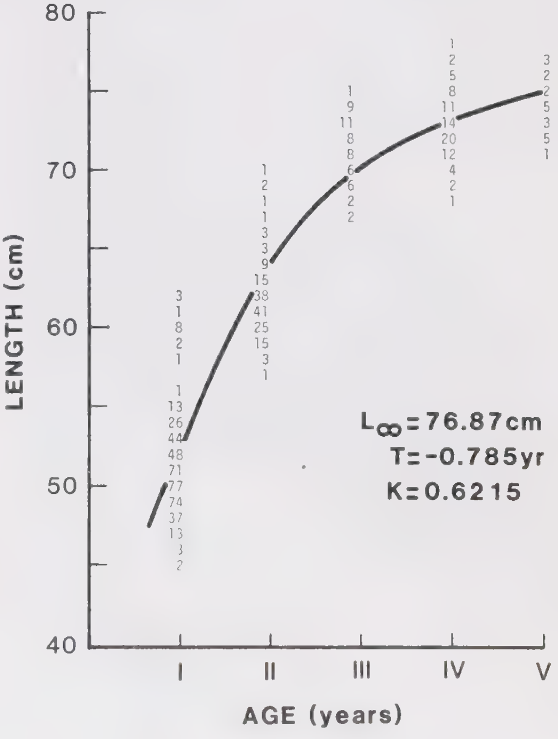

FIGURE 1.—Numbers-at-age by length in 1 cm intervals for the Pacific bonito, *Sarda chiliensis*. Data from 1973 California landings (Campbell and Collins 1975).

The length-frequency information and von Bertalanffy parameters are used to generate both deterministic and stochastic estimates of numbers-at-age. The estimated length-at-age

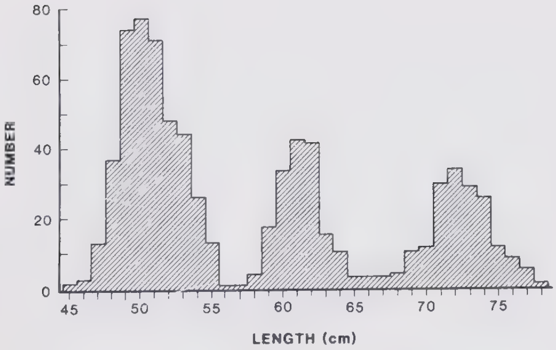

FIGURE 2.—Length frequency for the Pacific bonito, *Sarda chiliensis*, from 1973 California landings (Campbell and Collins 1975).

and sample standard deviations are

Age	*Length*	*Standard deviation*
I	51.5 cm	2.7 cm
II	63.3 cm	2.1 cm
III	69.5 cm	2.3 cm
IV	72.9 cm	2.0 cm
V	74.8 cm	1.9 cm

Deterministic estimates were made on lengths rounded to the nearest 0.1 cm. From Equation (2) the deterministic numbers-at-age are shown in column 3 of Table 2 with the difference between the true and estimated numbers in column 4. While the estimates are reasonably close over the first two ages, they become increasingly disparate for older ages. Thirteen fish had lengths greater than those at the maximum age. Seven had lengths greater than L and consequently were unclassifiable.

Quarter centimeter intervals were used to compute the stochastic estimates of age frequency. The results are shown in column 6 of Table 2, with the difference between true and estimated numbers in column 7. For all ages, especially the older ages, the stochastic estimates are closer and less biased than those of the deterministic method (column 3).

Some insight into the improvement of the stochastic age estimates over the deterministic age estimates can be gained by inspection of Figure 1. Lengths of age I fish overlap those of age II fish and vice versa. Since the deterministic cutoff point for age I fish is 58.7 cm (1.5 yr), all overlap is lost in the deterministic model. In contrast, for the stochastic model, overlaps in lengths-at-age are shared between ages, the degree of sharing being relative to the probabilities of length intervals at the respective ages.

With increasing age, the extent of relative overlap and, consequently, misaging increases for the deterministic model; allocation of lengths to ages becomes more sensitive. Only if the degree of overlap between adjacent ages is equal do accurate estimates of numbers-at-age result from the deterministic model. In the present example varying year-class strength and random variability in lengths-at-age offset this sensitive compensatory mechanism needed for accurate estimation with the deterministic model.

Fish lengths above 75.3 cm, the length at age 5.5 yr, are misclassified either as older or of infinite ages for the deterministic model. Since for the stochastic model probabilities of length intervals at age exist for all ages and lengths, even for lengths above L_∞, fish at lengths above the 75.3 cm cutoff point are distributed to all ages relative to their respective probabilities for length intervals.

DISCUSSION

Calculations of age from length via the von Bertalanffy growth equation result in several

TABLE 2.—Deterministic (col. 3) and stochastic (col. 6) estimates of numbers-at-age with their respective differences from the true numbers-at-age in columns 4 and 7 for the Pacific bonito, *Sarda chiliensis*, from 1973 California landings (Campbell and Collins 1975).

	Numbers-at-age						
Age (1)	True (2)	Deterministic (3)	Difference (4)	% Difference (5)	Stochastic (6)	Difference (7)	% Difference (8)
I	424	411	13	3.1	415	9	2.1
II	158	167	−9	−5.7	162	−4	−2.5
III	54	39	15	27.8	49	5	9.3
IV	80	71	9	11.3	85	−5	−6.3
V	21	29	−8	−38.1	26	−5	−23.8
>V	—	13	−13	Inf.	—	—	0.0
Inf.	—	7	−7	Inf.	—	—	0.0

types of bias. The degree of bias is proportional to overlap in lengths-at-age and changes with weak or strong year classes. When overlap increases with age, age-frequency estimates will generally be more biased for older than younger ages. When overlap occurs, biases will always result, since the numbers-at-length will be allocated to unreasonably old ages. Any numbers-at-length for lengths greater than L_∞ will be undetermined in age estimation, resulting in downward biases for those ages contributing such lengths.

Age estimation biases can be effectively removed by creating a stochastic model based on a matrix of length interval probabilities at age. The probability matrix (*P*-matrix) is independent of year-class strength and will effectively remove all sources of estimation bias except that due to random variation in length-frequency estimation. As long as the von Bertalanffy growth parameters remain the same over time, the stochastic method based on accurate estimates of variance in length-at-age will always yield unbiased results.

A probability model of the distribution of length-at-age with estimated parameters is necessary for estimating probabilities of length intervals at age for the *P*-matrix. If age information is unavailable then variances can be estimated from visually separable length-frequency modes. In the case where modes are separable for the first few ages only, there will be a problem in estimating variances for older ages: A model relating the variance in length-at-age with age can be used in estimating variances for these older ages. Ricker (1969) proposed that while distributions in lengths-at-age remain normal, variances increase during the first few years, stabilize, and then decrease over the final years. The trend in variances with age for a similar species might also be substituted in cases where variances are unavailable.

The principal strengths of the stochastic method are that few fish are required to be aged to estimate the *P*-matrix and that existing von Bertalanffy growth relations can be used. Accurate estimates of variance in length-at-age can probably be achieved with as few as 20 to 30 fish/age, which is likely to be a much smaller number of fish than needed to estimate accurate proportions of age-at-length necessary to construct an age-length key.

Von Bertalanffy growth parameters have been estimated for many species. Since most stocks have variant year-class strength, overlaps in lengths-at-age, and lengths exceeding the upper bound for the last age attainable, conversion to a stochastic model may be necessary, if unbiased estimates of age frequency are desired. Reexamination of age-length data used to estimate the von Bertalanffy parameters may be useful in estimating variances in lengths-at-age for the *P*-matrix. Taking additional age-length samples may be a cost-effective way of improving age-frequency estimation.

In fishery management, the overestimation of maximum age by the deterministic von Bertalanffy equation may produce underestimates of mortality rates which may result in overestimates of population size and recruitment. Further, the deterministic method tends to "fill in" weak year classes which results in underestimates of year-class variability and overestimates of recruitment stability. In general, all of these affect accuracy of a stock assessment and contribute to improper advice for fishery management.

Application of the stochastic method shown here to cover other growth equations and situations, such as discontinuous growth, is handled by simply estimating appropriate elements in the *P*-matrix for each case.

ACKNOWLEDGMENTS

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Effort Dynamics of the Northern California Dungeness Crab (*Cancer magister*) Fishery

LOUIS W. BOTSFORD

Department of Wildlife and Fisheries Biology, University of California, Davis, CA 95616, USA

RICHARD D. METHOT JR.[1]

Bodega Marine Laboratory, P.O. Box 247, Bodega Bay, CA 94923, USA

AND WARREN E. JOHNSTON

Department of Agricultural Economics, University of California, Davis, CA 95616, USA

BOTSFORD, L. W., R. D. METHOT JR., AND W. E. JOHNSTON. 1983. Effort dynamics of the northern California Dungeness crab (*Cancer magister*) fishery. Can. J. Fish. Aquat. Sci. 40: 337 – 346.

Knowledge of the dynamic response of fishing effort to abundance is essential to a complete understanding of the cycles in catch in the northern California Dungeness crab fishery. In this fishery there is a lagged response of harvest rate to changes in abundance that is caused either by a time lag in fishermen entering and leaving the fishery following changes in abundance, a lag in market expansion and contraction following changes in abundance, or a combination of both. The time lag in this response appears to have decreased over the past 30 yr. This lagged response is a potential cause of the cycles. However, neither of the two potential cyclic mechanisms examined here, a predator–prey mechanism (with man as the predator) and a price-dependent escapement mechanism (with price dependent on past catch), is a cause of these cycles. Although time-varying effort does not cause the cycles, it does have a substantial effect on the resulting catch record and population dynamics. If there is a density-dependent recruitment mechanism in this population as proposed earlier, the presence of this lagged response would cause the period of observed cycles to be longer than would be expected on the basis of population dynamics alone. Hence, previous estimates of the expected period of cycles from various population mechanisms are low. Removal of this response is a potential means of stabilizing this fishery.

Key words: effort, Dungeness crab, harvest rate, predator–prey, price, stability, age, cycles

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Une connaissance de la réponse dynamique de l'effort de pêche par rapport à l'abondance est essentielle à la compréhension complète des cycles de capture du crabe dormeur dans la Californie septentrionale. Dans cette pêche, il y a décalage entre les variations de l'abondance et le taux de capture, probablement attribuable soit à un décalage entre le temps que les pêcheurs commencent et finissent la pêche après les changements dans l'abondance, ou soit à un décalage dans l'expansion et le resserrement du marché après les changements dans l'abondance, soit à une combinaison des deux facteurs. Le retard de la réaction semble avoir diminué au cours des 30 dernières années. Cette réaction décalée est une cause potentielle de ces cycles. Toutefois, ni l'un ni l'autre des deux processus cycliques potentiels, soit une relation prédateur–proie (où l'homme est le prédateur) et une relation d'écoulement dépendante du prix (où le prix dépend des prises antérieures) n'est la cause de ces cycles. Quoique l'effort variant avec le temps ne cause pas ces cycles, il a une incidence importante sur le total des prises et la dynamique des populations. Si un processus de recrutement dépendant de la densité existe dans cette population, comme il a déjà été suggéré, la réaction décalée ferait que la période des cycles observés serait plus longue que ne le portait à croire

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[1] Current address (R.D.M.): National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038.

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la seule dynamique de la population. Donc, les évaluations antérieures de la période attendue des cycles d'après les divers processus relatifs aux populations sont faibles. L'élimination de la réaction est un moyen potentiel de stabiliser la pêche.

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THE catch record of the northern California Dungeness crab (*Cancer magister*) fishery is composed of cyclic fluctuations whose cause is not known. Although previous studies have focused on density-dependent (Botsford and Wickham 1978; McKelvey et al. 1980; Botsford 1981; McKelvey and Hankin 1981) and environmental (Peterson 1973; Botsford and Wickham 1975) phenomena as potential causes, little attention has been paid to changes in effort as a possible underlying mechanism. Methot and Botsford (1982) have recently shown that fishing mortality varies in a regular pattern with regard to catch. Fluctuations in effort are of interest not only because they are a potential cause of cyclic fluctuations in catch, but also because knowledge of the factors that determine effort each year (i.e. the dynamic behavior of fishermen, processors, and markets) is required to understand population dynamics adequately and to formulate fishery management policy.

The analysis described here was undertaken to (a) describe the dynamic response of effort to abundance and (b) determine the effect of that response on the fishery. First, the behavior of this fishery and the available data are described. Then possible mechanisms underlying the dynamic response of harvest to abundance are inferred by comparing actual behavior with expected behavior from proposed likely mechanisms. The possible effects of this response on population stability are then evaluated for several different assumed descriptions of population dynamics. In this context, the effect of the harvest response on the previously developed model with density-dependent recruitment is determined.

The Fishery

While the general behavior of the northern California Dungeness crab fishery can be readily described, the mechanisms that actually determine effort in the fishery are poorly known. The fishing season extends from December through June or July and only males larger than 159-mm carapace width can be landed. In most years more than 70% of the legal crabs are landed (Methot and Botsford 1982). Most of the landings are made in the first few months of each season. This is especially true in more recent years. As abundance has fluctuated there have also been fluctuations in price, number of boats, and actual harvest rates. The factors that govern the entry and exit of boats in the fishery during each season govern the fraction of crabs harvested each year.

There are a number of economic factors that could affect the number of crabs landed each year. The price at the beginning of the season is based on negotiations between fishermen and processors, and prices also change during the season. Processors have limited the number of boats and their landings during the recent periods of high abundance and the period of high abundance in the 1960s (D. Gotshall, P.O. Box 98, Avila Beach, CA 93424, personal communication). Average seasonal price generally varies inversely with catch and has increased over the past 30 yr, even when deflated to 1967 dollars by the consumer price index (Fig. 1).

The total number of boats landing crabs each season varies positively with catch with a small lag and has also increased over the past 30 yr (Fig. 2). However, this lag appears to have decreased in recent years. The fluctuation in number of boats in the fishery is related to the high mobility of the fleet; most of these boats also fish salmon and albacore. The number of boats in the fishery unfortunately is not necessarily a direct indication of annual fishing mortality. The actual pattern of harvest rate [based on annual catch and estimates of preseason legal abundance (Methot and Botsford 1982)] is also shown in Fig. 2.

Response of Harvest Rate to Abundance

The way in which harvest rate responds to changes in abundance can have a profound effect on the population. To interpret this response better, we first review the expected effects of the several different bioeconomic mechanisms known to be operating in the fishery, then compare the actual harvest rate record to these theoretical possibilities. From this comparison we can infer the possible mechanisms operating in this fishery.

Behavior of the fishery can be viewed in terms of a static relationship that changes only very slowly (e.g. with long-term changes in price) and a dynamic relationship that reflects the way in which the static "equilibrium" is reached after rapid changes in abundance. If the fishery were given enough time (i.e. a long enough season), the static equilibrium would be approached. At that time, a reasonable model would be that the value of a day's catch would equal the cost of obtaining that catch. Remaining abundance (escapement) would then be inversely proportional to price. From Fig. 1 price varies inversely with abundance. Hence escapement would increase with increasing abundance. The change in harvest rate with abundance would be

$$(1) \quad H = 1 - E(A)/A$$

where H = harvest rate, A = abundance, $E(A)$ = escapement at abundance A. The form of this static, equilibrium relationship between harvest and abundance is determined by the relationship between price, abundance, and escapement. For example, if the inverse relationship between price and abundance caused escapement to increase linearly with abundance, harvest rate would be constant. This relationship will change with long-term changes in price. If real price increases more rapidly than operating costs, escapement levels will decrease; hence harvest rates will increase.

Although this static equilibrium can be at least conceptually defined, it may rarely actually be reached because seasons are

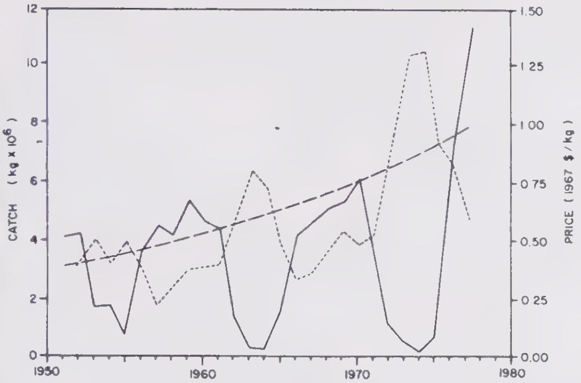

FIG. 1. Annual catch (—) and price (---) scaled for inflation (i.e. 1967 U.S. dollars). The exponential trend that was fit through these data and used to compute adjusted price is also shown (— — —).

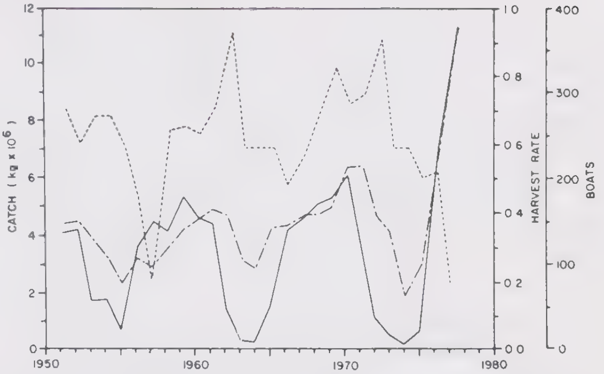

FIG. 2. Annual catch (—), total number of boats making deliveries (— - —), and harvest rate (---) computed from independent estimates of preseason abundance for the northern California crab fishery (Methot and Botsford 1982). (Note: abundance estimates for several years of high abundance (1957, 1966, 1977) were not significant. Hence, although abundance in these years is known to be very high and the values of harvest rate therefore low, the exact values of harvest rate used here are somewhat arbitrary.)

not infinitely long, and fishing capacity and market capacity can limit removal rates. In brief, there may not be enough effort to reach equilibrium before the season closes. If there is not enough fishing capacity (i.e. total boats or total crab pots), a rapid increase in abundance will result in initial low annual harvest rates that increase as more boats enter the fishery. Conversely, a rapid decrease in abundance will produce an initial increase in annual harvest rate followed by a decline. The overall effect would be counterclockwise rotation of the plot of harvest rate and abundance as shown in Fig. 3.

The precise dynamic behavior of this mechanism depends on such factors as price, opportunities in other fisheries, and the capacities of boats in the fleet. If price is high, one would expect that fishermen would maintain the ability to enter the fishery rapidly when abundance increases. Hence a long-term increase in mean price would be expected to result in less dynamic variation about the static equilibrium (i.e. less lag).

In addition to the influence of a lagged response of fishing capacity, a lagged market capacity can affect the harvest rate response in a similar way. As described earlier, processors change prices within seasons and also limit landings directly. During most years there are very few processors buying crab in each port. Few buyers operating under imperfectly competitive conditions characterize an oligopsonistic market. Each is keenly aware of the actions and reaction of the other buyers in the industry. Processing firms can expand and contract their activities in selected fisheries depending on potential profitabilities. Thus, they may respond to available abundance (supplies) in ways to maximize profits, entering a fishery when attracted by high profits, and vice versa. This behavior affects the effort response of the fishery. Suppose that the demand for crab by processing firms in an industry can be represented by the lower-most demand curve (identified as D_{normal}) shown in Fig. 4. If abundance (supply) is relatively low, price will be higher and quantity demanded lower, than under conditions of high abundance. Thus, if abundance has been low and then increases, processors will offer lower prices and purchase larger quantities. Other firms may then be attracted by the profitability of processing crab; their entry essentially shifts the demand curve to the right, increasing price paid to fishermen who respond to the price incentive by harvesting increased quantities. When abundance declines, the supply curves may shift leftward from $S_{\text{high abundance}}$ to $S_{\text{low abundance}}$, along the same demand curve. Prices continue to increase until enhanced profitability is exhausted, the marginal firms or plants exit the industry, and the demand for crab from the fishery shifts back to D_{normal} from D_{expanded}. The market contracts, and both prices paid to fishermen and quantity purchased by processors, fall. The dotted time path within Fig. 4 approximates the locus of prices and quantities over time caused by changes in abundance and the behavior of processors.

The effect of this mechanism on the harvest rate dynamics is a decrease in harvest rate following a rapid increase in abundance. As abundance remains high, catch increases because of market development, and harvest rate increases. When abundance decreases rapidly, catch decreases and harvest rate and price increase. As abundance remains low, price gradually decreases as the initial demand curve is approached, and harvest rate decreases. Thus the effect of this mechanism on the harvest rate versus abundance plot is indistinguishable from the response that resulted from a lagged fishing response. (The effect of a processor-imposed limit on landings is essentially the same as that of limited fishing capacity.) It can be distinguished, however, on the basis of the required increase and decrease in price within the high and low abundance periods, respectively. This pattern appears to be present in the high catch periods in the late fifties and sixties and the low catch periods in the early sixties and seventies (Fig. 1).

A third potential dynamic mechanism is of a completely different nature. It would occur under conditions such that fishing capacity was high enough to fish the legal population down each year to the price-determined level of escapement. However, a lag in the response of price to abundance would prevent the simple, static equilibrium described earlier. If price did not respond immediately to abundance, the response

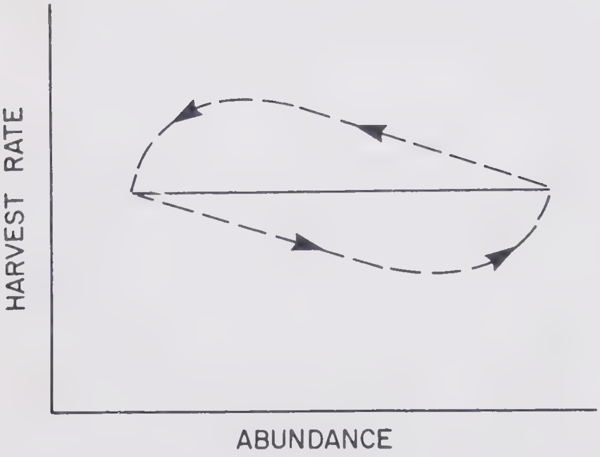

FIG. 3. A typical example of the static, equilibrium relationship between harvest rate and abundance (—) and the path that a fishery with a lagged effort response would follow (---).

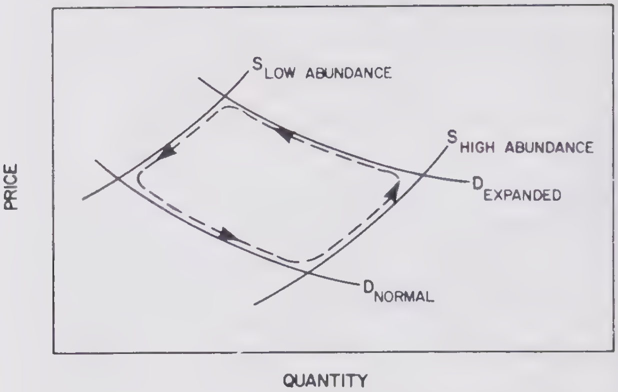

FIG. 4. Proposed changes in supply and demand curves with abundance. When moving between low and high equilibria the system moves initially along the appropriate demand curve (---). This curve shifts as high or low abundance is maintained.

of harvest rate to changes in abundance would be altered in a way that differs from those described previously. The response of price to changes in abundance could be delayed for reasons such as large stocks of frozen crabs held over from previous years.

A rapid increase in abundance with no change (or a slow change) in escapement (because of the slowly changing price) would lead to an initial increase in harvest rate followed by a decline to equilibrium as price decreased. The converse would occur following a rapid decrease in price, resulting in the clockwise rotation of the harvest rate, abundance plot shown in Fig. 5.

MECHANISMS PRESENT IN THE FISHERY

The plot of observed harvest rate and abundance (Fig. 6) does not follow a line of constant harvest rate but rather appears to rotate in a counterclockwise direction. Rapid increases in abundance (e.g. 1957, 1966) lead to low harvest rates, and rapid decreases in abundance lead to high harvest rates (e.g. 1962, 1972). As stated earlier, it is difficult to discern between a lag in fishing capacity and a lag in market capacity as the underlying cause of this behavior. However, the increase in price during periods of high abundance and decrease in price during periods of low abundance is commensurate with a lagged market response. As the observed behavior may be caused by either mechanism, they will be referred to collectively as a lagged effort response in the remainder of this paper.

The higher than usual value of the 1976 harvest rate is commensurate with the increase in real price of crabs. This could have resulted from a more rapid response of effort to increasing abundance because crabs were more valuable.

Any effect of lagged price on escapement is not significant enough to be apparent. The presence of a lagged response of price can be tested for in the price and catch data in Fig. 1. The correlation between adjusted price (1967 dollars with exponential trend removed, Fig. 1) and crab catch in previous years is significant at the 0.05 level at lags of zero and 1 yr but not at 2 yr (−0.739 and −0.453 and 0.063 at lags of zero, 1, and 2 yr, respectively). However, this correlation could stem from a negative correlation coefficient in year zero and highly autocorrelated catch. The partial correlation coefficient implies that the latter is the case. The partial correlation between price at time t and catch at time t given catch at time $t - 1$ is significant but the partial correlation between price at time t and catch at time $t - 1$ given catch at time t is not significant (−0.590 and −0.085, respectively).

Effect of Harvest Response on Fishery Behavior

The description of the response of harvest rate to changes in abundance can now be combined with descriptions of possible population behavior to determine the effect of harvest response on population level and the fishery as a whole. We will determine whether the harvest response is the cause of the observed cycles through either a predator−prey mechanism or price-dependent escapement with a lagged response of price to abundance, then evaluate the effect of harvest response on a population with density-dependent recruitment.

PREDATOR−PREY CYCLES

Predator−prey cycles with man as the predator involve the following sequence of events: abundance increases, effort increases after a certain lag, abundance then decreases as a result of increased effort, effort decreases in response to decreased abundance after a time lag, and finally, because of decreased effort, abundance increases to begin the next cycle. Both a lagged response of effort to abundance and a lagged response of abundance to effort are required. Mechanisms of this kind have been associated with cyclic behavior in other exploited populations [e.g. Gulland (1974), p. 17; Wilen (1976); Bell et al. (1977)].

Because a lagged response of effort to abundance has been shown to exist, we shall evaluate whether that mechanism can cause the observed cycles in a predator−prey fashion. Abundance each year will be the sum of recruitment and the result of escapement in the previous year. This can be represented by:

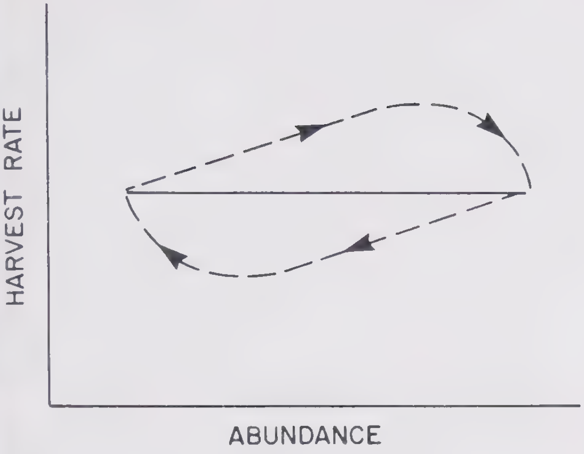

FIG. 5. The static, equilibrium relationship between harvest rate and abundance (—) and the path that a fishery with price-dependent escapement with price dependent on past catch would follow (---).

$$(2) \qquad A_t = A_{t-1}(1 - H_{t-1})\,G + R_t$$

where A_t = abundance in year t
H_t = harvest rate in year t
G = total change in biomass during a year (includes natural mortality and growth)
R_t = recruitment to legal size during the year prior to fishing season t.

For this simple representation, age structure is not included. Thus the major simplification of the model is that G is assumed constant when it would in general change with age structure.

This equation can be written in terms of the rate of increase

$$(3) \qquad r = A_t/A_{t-1} = (1 - H_{t-1})\,G + R_t/A_{t-1}.$$

In a cyclic population, changes in the values of H_t and R_t must cause the population to shift repeatedly between increasing and decreasing population size ($r > 1$, $r < 1$). Thus, whether this population is cyclic depends on the dependence of harvest rate on past abundance (described earlier) and the dependence of recruitment on abundance. We now evaluate the combination of harvest rate behavior described earlier with two different assumptions regarding recruitment: constant recruitment rate and recruitment rate proportional to abundance. (Density-dependent recruitment is evaluated in the next section.)

If recruitment rate is proportional to population size, in predator–prey cycles the population will increase from low levels because decreasing harvest rate is allowing a larger population to build up. If this were happening, there would be greater escapement at lower abundance. From Fig. 7 this is not the case. Higher escapement occurs at higher abundance.

If recruitment rate is constant in predator–prey cycles, the change in harvest rate itself must cause the shift between an increasing and a decreasing population. This does not appear to be the case because of the way that abundance changes. At low levels harvest rate drops from near 0.9 to near 0.5 with no change in abundance, then abundance suddenly increases.

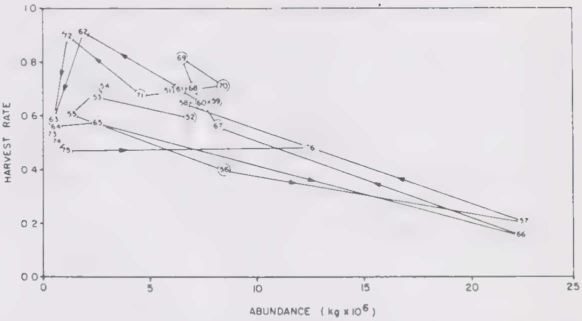

FIG. 6. Actual annual harvest rates plotted versus actual abundance for the northern California Dungeness crab fishery. (Because abundance estimates for 1957 and 1966 were not significant, the exact position of these points is somewhat arbitrary. However, abundance was unusually high and harvest rate was unusually low.)

There is again no gradual increase in abundance evident in the escapement at low levels.

The only remaining alternative is that recruitment is higher at low population levels and vice versa (i.e. density-dependent). Again the lack of gradual increase in population level (escapement) at low levels implies that for this mechanism to be significant a lagged response of recruitment to abundance is required. However, even if that were the case, it does not seem likely that the slight changes in harvest rate seen here are enough to be controlling abundance. The changes in harvest rate at high abundance levels are not large enough to cause the observed declines in abundance. Thus, even though a lagged recruitment response may be present, it does not appear to interact with harvest rate to cause predator–prey cycles.

From these considerations we can conclude that changes in harvest rate in response to abundance are not the primary cause of fluctuations in abundance in a predator–prey fashion. However, we have not discounted the possibility that they may influence population behavior significantly by exacerbating instability caused by other mechanisms.

PRICE-DEPENDENT ESCAPEMENT WITH LAGGED PRICE RESPONSE

Though there was little evidence for a lagged response of price to past catch or abundance and the behavior of price-dependent escapement with a lagged price response did not appear to be dominant in Fig. 6, analysis of stability of this mechanism is presented briefly because it may apply to this fishery in the future or to others. If escapement depended inversely on price, as described earlier, and price was influenced by previous catch (e.g. due to storage of past catch by processors and marketers), then catch could be cyclic. As abundance increased, high catch would lead to low prices which would result in high escapement and low catch. When abundance decreased, low catch would eventually lead to high prices which would result in low escapement and high catch, and the cycle would then repeat.

To analyze stability of this mechanism, we assume that escapement each year depends (possibly in a nonlinear fashion) on a weighted sum of total catch in previous years.

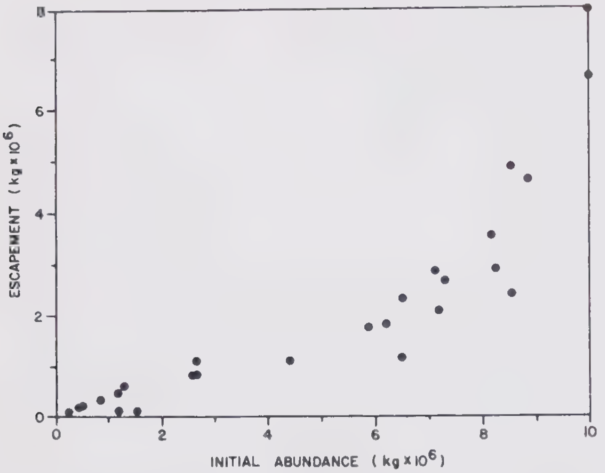

FIG. 7. Annual escapement and initial abundance estimates for the years 1955 through 1976 in the northern California Dungeness crab fishery.

$$(4) \quad (1 - H_t) A_t = g\left[\sum_{s=1}^{T} k_s H_{t-s} A_{t-s}\right]$$

where k_s = a constant specifying the relative effect of catch in the sth previous year on escapement in the current year ($s = 1, 2, \ldots T$). In the crab fishery, for example, g would be an increasing function of its argument (i.e. as catch in previous years increases, market price is depressed and escapement increases).

By defining catch to be

$$(5) \quad C_t = A_t H_t,$$

we can express the equations (2) and (4) as

$$(6) \quad C_t = Gg\left[\sum_{s=1}^{T} k_s C_{t-1-s}\right] - g\left[\sum_{s=1}^{T} k_s C_{t-s}\right] + R_t.$$

This expression has the intuitively satisfying interpretation that catch is growth per unit biomass (G) times last year's escapement minus this year's escapement plus this year's recruitment (R_t). The fact that catch is the weighted difference between two lagged escapements critically affects dynamic behavior of this system.

The derivation of the conditions under which this model would be unstable and the catch record that would result are in the Appendix. The relevant result here is that for a wide range of reasonable forms of the dependence of price on past catch, any unstable cycles produced will be of period two. Intuitive support for this result can be gained from equation (6). Catch depends on the difference between a function (g) of past catches at different time lags (time lags in the first term are shifted backward in time by 1 yr with respect to time lags in the second term). Because of this, in the dynamic behavior of this system each lagged catch is approximately cancelled by its corresponding component in the other term. There is only one term left uncancelled, the term involving catch at a lag of 1 yr. Only cycles of period two can result from a lagged response at 1-yr lag.

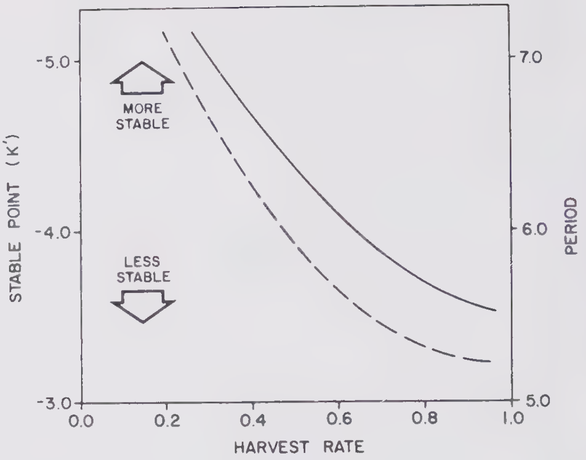

FIG. 8. The stable point K' (---) and the period of cycles produced (—) for a discrete time model with density-dependent recruitment as the (constant) annual harvest rate is varied.

A second result of this analysis is that if price depends significantly on the present value of catch in addition to past values of catch, the system becomes much more stable. Because of these two results, it is not likely that this mechanism is causing the observed periodic fluctuations in catch.

DENSITY-DEPENDENT RECRUITMENT

Density-dependent recruitment is one of the possible causes of the observed cycles in the northern California crab population. The stability and behavior of an age-specific model with density-dependent recruitment and constant effort were analyzed by Botsford and Wickham (1978) in relation to this population. However, the results obtained by them assumed constant effort, hence, do not hold for the time-varying effort identified here. To determine whether the density-dependent recruitment mechanism is present in this population, the behavior of a model that includes the dynamic response of effort to abundance must be known.

The results obtained by Botsford and Wickham (1978) were in terms of (a) the stability inherent in the age structure of the population and (b) the period of cycles produced. In their model recruitment was the product of total reproduction and a recruitment survival function that depended on effective population size. Stability depended on the relative values of the normalized slope of the density-dependent recruitment function (i.e. the amount that the recruitment survival function changed with a change in population size) and the inherent stability of the population age structure. The general result was that a population with a greater number of age-classes was usually more stable (i.e. could tolerate a steeper slope of the recruitment survival function) than a population with fewer age-classes. The period of the cycles was shown to be roughly twice the mean lag between the age at which the inter-age, density-dependent effect acts on younger animals and the age at which older animals cause this effect (i.e. approximately the mean age of those individuals causing

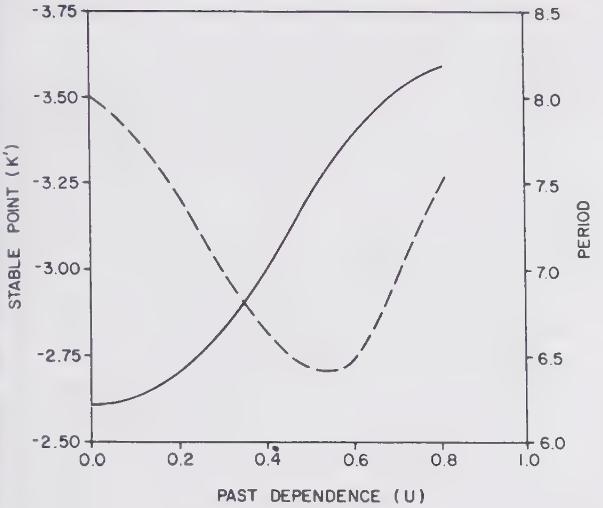

FIG. 9. The behavior of the stable point K' (---) and the period of cycles produced (—) by the discrete time model with density-dependent recruitment with constant effort replaced by a lagged response of harvest to abundance as the degree of lagged response is varied from $U = 0$ (constant effort) to higher values.

density-dependent recruitment).

These characteristics are reflected in the values of period and stable point obtained through simulation of a discrete-age version of the baseline model (with reproduction) presented in Botsford and Wickham (1978) (Fig. 8). The stable point K' is the minimum value of slope of the density-dependent recruitment function that can be tolerated before the population becomes unstable. Hence, a more negative value of K' corresponds to an inherently more stable population. As the level of constant effort increases, the relative number of age-classes decreases (i.e. older age-classes are depleted), and the population becomes less stable. Also, because the mean age of the population decreases with increased effort, the period of the cycles decreases.

Though we don't know the specific mechanism causing the response of harvest rate to abundance, we can evaluate the effect of this response on population stability through a simple model that mimics harvest rate dynamics. Define

(7a) $C'_t \equiv H_{\text{norm}} A_t (1 - U) + C_{t-1} U,$

(7b) then let $C_t = C'_t \qquad C'_t < H_{\max} \times A_t$

(7c) $C_t = H_{\max} A_t \qquad C'_t \geq H_{\max} \times A_t$

where U = a constant $(0 \leq U \leq 1.0)$
C_t = catch in year t
A_t = abundance in year t
H_{norm} = equilibrium harvest rate
$H_{\max}$ = maximum harvest rate.

In this model, catch is a weighted sum of abundance harvested at a rate of H_{norm} and last year's catch (7a), except that harvest rate is constrained to be less than $H_{\max}$ (7b and 7c). The constant U reflects the relative dependence of harvest rate, and therefore catch, each year on the previous year's catch (i.e. the relative inertia or lag in the response).

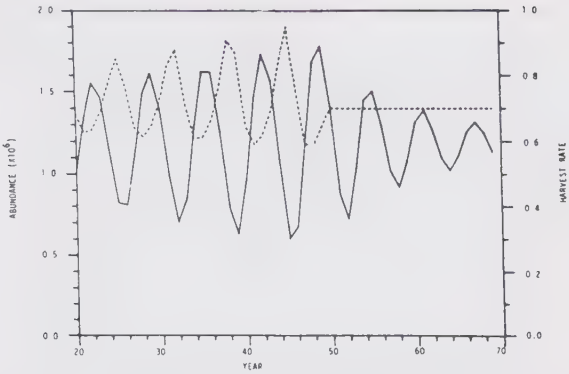

FIG. 10. An example of increased stability through removal of a lagged effort response. Catch (—) and harvest rate (---) are initially fluctuating in an unstable fashion. When harvest rate is set to a constant value for $t > 60$ yr, the population becomes stable.

For values of H_{norm} and $H_{\max}$ that produce a typical pattern of harvest rates, as the value of U is varied from 0.0 (a constant harvest rate) to higher values (greater past-dependence), the period of the cycles produced increases (Fig. 9). The inherent stability of the model also decreases up to $U = 0.8$ at which it increases. Because it is not likely that current catch depends to such a large degree on past catch, this value is probably beyond the values that produce a reasonable model of the actual response. Thus, over the reasonable range of values, stability decreases with increased dependence of the effort response on previous catch.

Discussion

The dominant response of effort in this fishery over the past 30 yr is one of considerable inertia or resistance to rapid change. The dramatic increases and decreases in abundance are not perfectly "tracked" by the catch record. This effect is caused by two limitations on the rate of "outflow" from the population to the consumer. The first is the limited number of boats or crab pots. Because of the limited capacity of each boat, catch cannot change dramatically until the number of boats or pots changes. The second limitation is the rate at which processors will accept crabs. This rate is prevented from changing rapidly by economic factors. The relatively small number of firms in the industry can engage in collusion to protect or increase profits by limiting quantities. As these two limiting mechanisms, fishing capacity and market capacity, operate in series, either one of them can be the "limiting factor" at different times.

The lack of significance of a price-dependent escapement mechanism with past-dependent price is somewhat unexpected. Escapement does appear to increase with the inverse of adjusted price as would be expected if the population were reduced to the zero-profit level each year. That the plot of harvest rate versus abundance (Fig. 6) does not reflect this type of fishery is primarily because of the years following a rapid increase or a rapid decline in abundance (i.e. 1956, 1966 and 1962, 1972). The dependence of price on past catch is expected because of the stores of frozen crab that are left from year to year in processors' lockers. A possible explanation for the absence of this relationship is that a prediction of abundance (based on a preseason cruise) was available before the price negotiations that preceded each season. This could have shifted dependence on past catch to dependence on the (expected) present catch. A second possibility is the adjustments in price that are made during most seasons. They would also shift price-dependence toward the present.

The lagged effort response in this fishery appears to be less prevalent in recent years. This would be expected on the basis of the increase in real price. (The general increase in real price is not confined to this fishery but has also occurred in others in recent years.) As price increases, the lag in response of fishing capacity will decrease because of the increasing advantage of maintaining the ability to enter the fishery rapidly. The increasing value of crabs will also induce other processors to enter the fishery, thus decreasing the lag associated with market response.

The trend in the influence of effort response on this fishery appears to be generally toward increasing stability. Decreased lag increases stability of predator–prey mechanisms and the density-dependent recruitment mechanism. The fact that instability can arise with no lag in effort, because of the price-dependent escapement mechanism with past-dependent price, does not contradict this general trend. Instability from this mechanism is of a special kind. It occurs in what would be a stable region in continuous time and is possible only because this system is defined in terms of discrete time. This is reflected in the fact that cycles arising from this mechanism would be of period two. Thus, the overall trend is toward greater stability.

Other mechanisms may influence effort in this fishery. Botsford et al. (1982) analyze a cyclic covariation of California salmon catch with crab catch. Salmon catch peaks when crab catch is increasing. Because crab and salmon seasons do overlap, high salmon catch could contribute to low harvest rate during years of increasing crab abundance. Also, in recent years, limitations on entry into other fisheries have induced fishermen to make a couple of landings in fisheries that are not yet limited (such as the crab fishery), merely so that they can maintain the option of later participating in that fishery on a larger scale even if entry is eventually closed.

The impact of the lagged response on stability of a population with density-dependent recruitment is relevant both to the issue of the cause of the cycles and future management of the fishery. The stability results obtained seem intuitively reasonable. Earlier work using constant effort showed that stability increased as effort decreased causing the relative numbers in older age-classes to increase. The period also increased as the numbers in older age-classes increased. As one replaces constant effort with a lagged response of effort to catch, one would expect a decrease in stability because a lagged feedback system is being allowed to overshoot the equilibrium by a greater amount. Conversely, a decrease in the lagged effort response allows less overshoot, hence would be expected to stabilize the system. This reasoning holds until the lag becomes so great ($U = 0.8$) that the increased overshoot allows a substantial increase in the number of older individuals in the population. From the constant effort results, we know that this acts to stabilize the population.

The results in Fig. 9 appear to be robust to variations in $H_{\max}$ and H_{norm} over ranges of values that match observed harvest rates. Slight variations in $H_{\max}$ do not substantially change results. Varying H_{norm} to 0.5 or 0.7 produces a less stable population at 0.7 and a more stable population at 0.5, as would be expected on the basis of constant effort results (Fig. 8). The pattern of changes in stability as U is varied is preserved.

The new result, that the period of cycles produced by density-dependent recruitment increases with a lagged effort response, has important implications for the determination of the cause of the cycles. Botsford and Wickham (1978) noted that the period of observed cycles was greater than the period of cycles produced by a model with constant effort, current estimates of life-history parameters, and the density-dependent recruitment effect occurring near the time of post-larval settlement. The last characteristic would be the case if cannibalism were the density-dependent mechanism. McKelvey et al. (1980) pointed out the same disparity between model periods and observed periods, using a different model with discrete time and age. They chose, however, to reject cannibalism as a potential cause of the cycles on that basis. [See Botsford (1981) and McKelvey and Hankin (1981) for further discussion.]

The fact that the observed lagged effort response can cause an increase in period of 25% (Fig. 9, constant effort versus $U = 0.6$) is an example of a previously unknown mechanism that can have a significant effect on the period of observed cycles. As such, it underscores the potential hazards of rejecting mechanisms because they do not satisfy a certain model when it is not known whether the other parameters and structure of the model accurately mimic the real population (Botsford 1981). Thus, this result casts doubt on both the specific rejection of cannibalism as a cause of the cycles by McKelvey et al. (1980) and the general form of argument used in doing so.

A second feature of the stability results is their potential use in management. The fact that removal of a lagged response can make the population more stable leads directly to consideration of employment of this fact in management. If the amount of effort (or catch) could be increased over its present value during high years and possibly lowered during low years, the population could stabilize at a constant value. The increase in effort following an increase in abundance could possibly be brought about by better prediction of good years and early market development or reduction of the oligopsonistic nature of the fishery. (The latter would probably increase overall value of the fishery even if stability were not affected.)

The potential effect of this behavior can be demonstrated by simulating the fishery using a lagged effort response [equation (7)] then switching to constant effort (Fig. 10). In this example, removal of the lagged effort response caused the population to become stable. The actual change in harvest policy required to stabilize the crab fishery (if it is possible) requires further definition of the population and the fishery. The possible policies examined should not be confined to those that would return the system to constant harvest rate but rather should include schemes which go beyond that to policies that include higher harvest at high abundance and lower harvest at low abundance. Other simulations have shown that these policies can have an even stronger stabilizing effect than just removing the lag.

This scheme would be beneficial in spite of the fact that the actual cause of the cycles is unknown. If the cycles were caused by environmental factors rather than density-dependent recruitment, long-term landings from the fishery would probably be increased even though the population would not stabilize at a constant value. A policy such as this could also serve as a test of several potential causes of the cycles. If the population were stabilized by such a policy, then density-dependent mechanisms that involve only the unfished females and mechanisms involving the environment could be rejected. A gratuitous observation on the stabilizing effects of diminished lag is that the decrease in lag that has accompanied the long-term increase in market price could possibly stabilize the fishery without actual policy changes.

The influence of a lagged fishery response on stability of models with density-dependent recruitment has shed some light on mechanisms underlying cycles and provided a potential management approach. However, both the identification of the cyclic mechanism and the eventual advisability of such a management scheme depend critically on further definition of the life history parameters of the crab and the influence of environmental variables on this population.

Acknowledgments

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Appendix

The approach to stability analysis is to determine conditions for local stability of a linearized version of the model in terms of small variations about an equilibrium point. If the linearized model is stable, the model is locally stable. If the linearized model is unstable, the model is locally unstable. The condition of equilibrium, assuming recruitment, is

$$\text{(A-1)} \quad C_e = g\left[C_e \sum_{s=1}^{T} k_t\right](G - 1) + R_t.$$

From the definition of a small variation in catch about equilibrium,

$$\text{(A-2)} \quad \Delta C_t = C_t - C_e$$

and from equations (6) and (A-1) the linearized model can be expressed as

$$\text{(A-3)} \quad \Delta C_t = g'\left[C_e \sum_{s=1}^{T} k_s\right] \sum_{s=1}^{T+1} h_s \Delta C_{t-s},$$

where $g'(x) = dg(x)/dx$

$$h_s = -k_1 \qquad s = 1$$

$$h_s = -k_s + Gk_{s-1} \qquad 1 < s < T$$

and $$h_s = Gk_T \qquad s = T.$$

The coefficients (h_s) of lagged values of the variation in catch are the difference between the coefficients (k_s) describing the influence of past values of catch on escapement and G times these same coefficients lagged by one time interval. This implies that if the values of k_ss decrease by a certain fraction for each interval (i.e. $k_{s+1} = pk_s$, $0 \leq p \leq 1$), for values of p near the value of G, h_s is very small for all $s > 1$. Stability will than be determined by k_1 and the system will behave as one that depends only on the past year's catch. Stability conditions for this simple case are similar to other familiar models (e.g. the single age-class stock–recruitment model). The system will be stable if $g'k < 1$, unstable if $g'k > 1$, and the response will be cyclic with period 2 yr.

Determination of stability for cases other than this simple case is more difficult. If escapement depends on catch up to n yr in the past, analysis of an nth order system is required. However, by assuming that the dependence of escapement on past catch decreases by a fixed proportion each year, we can simplify the analysis considerably.

We define a new variable S_i that could physically be the biomass of crabs in storage for i yr. We then assume that the amount in storage decreases by a fixed proportion each year

(A-4) $S_i = p^i C_{t-i}$.

This enables us to express the system in terms of only two variables S_1 and

(A-5) $S = \sum_{i=1}^{l-1} p^i S_i$.

The equations describing the system are

(A-6) $S_1' = g[S]G - g[pS_1 + pS]$

(A-7) $S' = p(S_1 + S)$

where the primes denote values in the current year and unprimed variables refer to the values in the previous year.

From the modified Schuur–Cohn criterion (Freeman 1965), also called the Jury test (Lewis 1977), we obtain the necessary and sufficient conditions for stability.

(A-8) $g' < \dfrac{1 - p}{-p\,(2p - 1 - G)}$

and

(A-9) $g' < \dfrac{1 - p}{p\,|2p - G|}$.

The system will be unstable if either of these is violated. Note that for $p = G$, the first condition reduces to $pg' < 1$, the same condition as arrived at above from the observation that the system would behave as if there were only a single lagged response after 1 yr. From equations (A-8) and (A-9), stability of this model depends on the relative values of G, g', and p. As stated earlier, p, the fraction of stored stock not sold each year, varies between 0.0 and 1.0. The value of g', the change in escapement with a change in past catch, is positive for a compensatory relationship between escapement and past catch. The value of G, the relative growth rate of biomass from 1 yr to the next, depends on growth and survival of the species as well as fishing effort.

Stability conditions [equations (A-8) and (A-9)] were verified by simulation for a range of values of p. Values of G were computed from estimates of growth and survival rate of the crab population (Botsford and Wickham 1978). Unstable behavior was always cycles of period two. Addition of the dependence of price on current catch increased stability by a factor of two if the weighting of present dependence was equal to the weighting of catch 1 yr in the past, and by a factor of 10 when the weighting of present catch was doubled. Thus the system is much more stable when price depends on present catch.

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Sea Level Variations at Monterey, California

DALE EMIL BRETSCHNEIDER and DOUGLAS R. McLAIN[1]

ABSTRACT

Sea level data from Monterey, Calif., during the period 1963 through 1976 were compared with data from coastal stations from Peru to Alaska. Sea level fluctuations at Monterey were correlated with data from these stations, particularly those to the south. The causes of sea level fluctuations at Monterey were investigated by correlation, regression, and spectral analysis of sea level with atmospheric pressure, zonal and meridional wind stress, Ekman and Sverdrup transport, surface temperature and salinity, and dynamic height data from nearby locations. Of these variables, dynamic height was the best predictor of sea level fluctuations. Atmospheric pressure, surface temperature, and meridional wind stress were of secondary importance. The prediction was better during the Davidson Current period than during the upwelling period.

INTRODUCTION

Sea level and its fluctuations have interested man for centuries. Historical sea level time-series data are unique among marine data sources in that they have been obtained continuously and inexpensively over periods of decades or longer at many coastal and island locations worldwide. Sea level records include not only periodic fluctuations due to astronomic tides but also nontidal, low frequency fluctuations resulting from various oceanic and atmospheric processes. The nontidal components can be isolated by filtering out the astronomic tides, thus making measurements of sea level useful as a spacially integrated index of nearshore and offshore ocean changes.

This paper examines the character of sea level anomalies at Monterey, Calif., and the relative importance of the large-scale atmospheric and ocean processes which may cause nontidal, low frequency fluctuations. An understanding of these processes will allow the use of the abundant historical records of sea level data to reconstruct changes in the past oceanographic environment of the California Current system, which, in turn, may aid in understanding past changes in distribution, abundance, and availability of marine fish populations. In particular, the study was designed to examine the utility of sea level data for identification of anomalous environmental periods and for monitoring of changes in coastal oceanographic conditions.

EARLIER STUDIES ON SEA LEVEL VARIATIONS

Sea level variations along the Pacific coast and their relationship to various environmental phenomena have been examined from a number of different points of view. In addition to the well-understood astronomically induced periodicities, it is widely recognized that coastal sea level measurements are influenced by: 1) wind waves and swell, 2) wind set-up or set-down against the coast due to storms, 3) changes in atmospheric pressure over the ocean surface, 4) redistribution of water mass due to wind stress, 5) changes in average density of the seawater column, 6) long period astronomic tides, 7) subsidence or uplift of the land upon which the tide gage is located, and 8) changes in total mass of water in the oceans associated with the glacial ice budget. These physical processes are discussed by Montgomery (1938). LaFond (1939) found close agreement between weekly mean sea level measured at La Jolla, Calif., and offshore geopotential topography, thus directly relating ocean currents to sea level. Jacobs (1939) suggested that the relationships observed by LaFond were not entirely due to changes in the density of surface water but rather to actual slopes induced by wind-driven water transport along the coast. Pattullo et al. (1955) found that south of lat. 40°N in the North Pacific Ocean, the seasonal variation of steric elevation and sea level are in phase, both having a maximum elevation in late summer or early fall and a minimum elevation in winter. This they took as a consequence of seasonal heating and cooling. These investigators further found that seasonal variations in sea level north of lat. 40°N along the northwest coast of the United States could not be explained by steric considerations alone, suggesting that nonisostatic processes such as wind and currents can lead to appreciable regional deviations. Roden (1960) used autocorrelation and spectral techniques to examine the relationship between monthly mean sea level pressure, wind, and sea surface temperature (SST) at several stations along the Pacific coast. He found good coherence between anomalies of sea level and atmospheric pressure, moderate to poor coherence between SST and sea level depending on the location of the station, and moderate coherence between anomalies of sea level and north-south component of the geostrophic wind. Sturges (1974) found high correlations between occasional steric observations and 3-d mean sea levels at Neah Bay, Wash., and San Diego, Calif. Reid and Mantyla (1976) demonstrated that the winter increase in seasonal sea level elevation along the northern North Pacific coast results from increased overall flow in the North Pacific subarctic cyclonic gyre.[2]

OCEAN AND ATMOSPHERIC PROCESSES NEAR MONTEREY

Monterey Bay is located along the central California coast, about 120 km south of San Francisco. The bay, which is bisected by a deep submarine canyon, is a large, semi-elliptical coastal feature measuring about 37 km wide at the mouth and about 19 km from the mouth to the innermost point.

The bay lies inshore of the broad, diffuse, southward flowing California Current. The strength of the Current is affected by the winds over the Current which, in turn, are controlled by the strength and location of the Aleutian low-pressure cell located over the Aleutian

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[1] Southwest Fisheries Center Pacific Environmental Group, National Marine Fisheries Service, NOAA, P. O. Box 831, Monterey, CA 93940

[2] After this paper was completed, the thesis of Chelton (1980) became available The reader is referred to it for additional information on processes affecting sea level along the coast

Islands, the Pacific high-pressure cell located east of the Hawaiian Islands, and the thermal low-pressure cell located in summer over the western United States. During spring and summer the Aleutian low normally weakens and the Pacific high intensifies and moves northward. Winds over the Current during this period are mainly from the northwest and are strongest when the Pacific high and thermal low-pressure cells are closest together and relatively intense. Winds weaken or change direction as this pressure gradient decreases. The seasonal change in strength and location of these pressure cells thus causes seasonal changes in the winds (Reid et al. 1958).

Skogsberg (1936) described three distinct phases or periods in the seasonal hydrography of Monterey Bay. The calendar year opens in the countercurrent or Davidson Current phase. In late fall and early winter of most years, winds are weak and variable and intermittent southerly winds occur. A northward flowing countercurrent is present at the surface close inshore off central California. The general north-northwest to south-southeast trend of the coastline and Ekman transport of surface water to the right of the wind cause onshore transport of surface waters and piling up against the coast. Minimal solar radiation and strong vertical mixing of surface waters by winter storms decrease SST's to a seasonal minimum during January or February. While SST's decline during the Davidson Current period, temperatures at deeper levels slowly increase due to advection of warm waters from the south. For example, temperatures at 50 m depth reach a seasonal maximum during December and January (Skogsberg 1936; Bolin and Abbott 1963). The end of the Davidson Current period is variable and difficult to pinpoint. About March, the offshore high pressure cell intensifies and northwest winds become frequent. The resulting Ekman transport causes offshore transport of surface water and, in the nearshore region, some of this water is replaced by cold, nutrient-rich subsurface water upwelled from the upper hundred or so meters. Upwelling is strongest when northerly winds are strongest, and near Monterey usually reaches a maximum in May or June (Bakun 1975). By August, northerly winds begin to slacken and the strong solar radiation of late spring and summer results in a steady rise in SST that usually continues through September. A period of calmer winds that Skogsberg (1936) called the oceanic period occurs in September and October. With a slackening of wind stress, the cool, upwelled water begins to sink and is replaced by warmer surface water from offshore. Coastal SST's rise to their highest seasonal values and strong vertical temperature gradients form (Bolin and Abbott 1963).

Thus the oceanographic regime off Monterey is marked by three distinct periods: the Davidson Current period, occurring during November through February, has weak northerly winds, strong winter storm events, northward current flow, and onshore transport of surface water. The upwelling period, occurring in March through August, has strong northwest winds, southward current flow, offshore transport of surface water, and upwelling of cool, nutrient-rich water. The oceanic period, occurring during September and October, is a period of calm between the northerly winds of the upwelling period and the southerly winds of winter. During this period, highest surface temperatures and strongest vertical temperature gradients occur. Although these are the average seasonal characteristics in the meteorological and oceanic regimes affecting Monterey Bay, there are marked year-to-year differences in both timing and intensity of the events.

DESCRIPTION OF DATA

Recorded tide data from the tide station at Monterey, Calif. were chosen for analysis because the tide gage lies along the biologically productive upwelling region off central California and is exposed to open ocean conditions with no nearby river discharge that may affect sea level measurements (such as at San Francisco or Crescent City, Calif.). The Monterey gage is the only primary tide station maintained by the National Ocean Survey (NOS) between San Francisco and Avila, and thus fills a large data gap along the central California coast. The Monterey station has been operated continuously since 1963 by the Naval Postgraduate School (NPS) but the time-series data have not been fully analyzed. The tide station is located along the southern edge of the bay near the end of Monterey Municipal Wharf No. 2 where the water has a depth of approximately 6.8 m. Because of the open shape of the bay and the narrow width of the continental shelf, tide measurements obtained here are presumed to approximate those of the open coast.

In addition to sea level data, meteorological and oceanographic data representative of the Monterey area, including surface atmospheric pressure data, geostrophic wind data, surface salinity and temperature data, and deep hydrocast data were used in this study. The geographic proximity of the various data sources allowed direct comparison of variables with minimal problems resulting from spatial distortion. Figure 1 shows the location from which each of the data sources was derived, along with bathymetric contours.

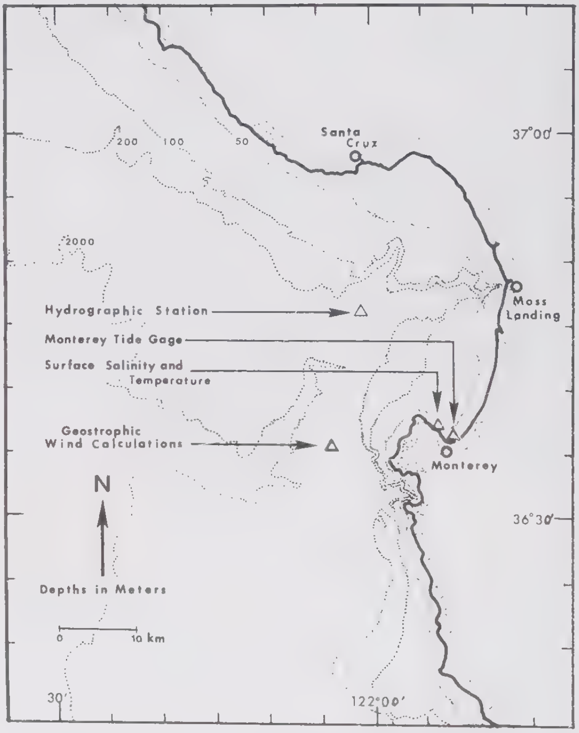

Figure 1.—Map of Monterey Bay, Calif., region showing location of data sources.

Monterey Sea Level Data

Tide Gages.—A standard recording tide gage, which traces tide heights continuously on a strip chart, was installed at the Monterey tide station by NPS personnel in June 1963. This analog system is entirely mechanical and is highly dependable when maintained properly. A drum-mounted strip chart is rotated by a spring-driven clock mechanism, and a pencil records sea level changes by means of a float-pulley system. A second instrument, a Fisher-Porter digital tide gage, was installed adjacent to the analog gage by the NOS in November 1973. This is an electrically operated system which punches digital data on foil tape. Both gages use the same 21.6 cm diameter float and have operated simultaneously since November 1973. The stilling well, which serves as a low pass filter for oscillations with periods greater than a minute, consists of a 30.5 cm diameter steel pipe with a 2.5 cm diameter orifice at the bottom. Both gages are checked for accuracy of time and height and are annotated about five times per week.

Data Processing and Reduction.—Continuous tide traces obtained from the analog gage during the period 20 July 1963 through 31 December 1974 were manually digitized for use in this study by Ocean Data Systems, Inc., Monterey, Calif. Datums were reviewed and data were reduced to hourly sea level heights using standard NOS procedures (Coast and Geodetic Survey 1965). Data from the digital gage for the period 1 January 1974 through 31 September 1976 were processed for hourly heights by the NOS and provided for use in this study. Data from both gages were recorded in feet and in this study converted to centimeters. The hourly heights from both analog and digital gages are accurate to about 0.1 ft (3.0 cm) and times of observation (Pacific Standard Time) are accurate to within 6 min. A small percentage of the hourly sea level data was missing, either rejected as erroneous or lost due to equipment malfunctions. As a result, some monthly means contain less than a full month of data. Missing data of duration of a day or longer are listed in Appendix A.

All hourly heights were measured relative to the station datum established by the NOS in November 1973. Mean sea level for the period 1963 through 1978 lies at 184.4 cm and the National Geodetic Vertical Datum lies 182.88 cm above the station datum.

Merging of Analog and Digital Tide Data.—To obtain the longest possible continuous tide record, it was necessary to merge the older analog data with the more recent digital data. Before the data sets were combined, the response of the two gauges was analyzed by comparing the hourly heights from both tide records for the calendar year 1974. The correlation coefficient between the analog and digital data sets exceeds 0.99, as anticipated.

The differences (digital-analog) between the two sets of hourly sea levels for the calendar year 1974 had a mean value of -0.06 cm. The frequency distribution of the differences (Fig. 2) resembles a normal distribution, with a standard deviation of 3.7 cm. Nearly all of the differences can be attributed to the fact that the digital data were recorded as instantaneous values, which can include short-term sea level fluctuations such as long period waves and seiches, whereas in the analog data, these short-term fluctuations were filtered out by manually smoothing the tidal curve before digitizing.

It was concluded that differences between the two data sets were negligible, and that the analog and digital data could be combined without significant error. Thus, analog data from the period 20 July 1963 through 31 December 1974 were combined with digital data from the period 1 January 1975 through 31 August 1976 to form a 13-yr time series containing 107,954 hourly observations.

Long Period Sea Level Changes.—Tide gages monitor the height of the sea level relative to land. Thus, changes in mean sea level over periods of years or decades can result from the addition or removal of water from the oceans due to global climatic variations, from subsidence or emergence of the land upon which the gage is located, or from long-period astronomic tides. For example, some long-period trends in sea level records, such as the rise in sea level in Panama described by Roden (1963) or the drop in sea level in the Juneau, Alaska, area described by Hicks (1973), clearly result from local or regional land subsidence or uplift.

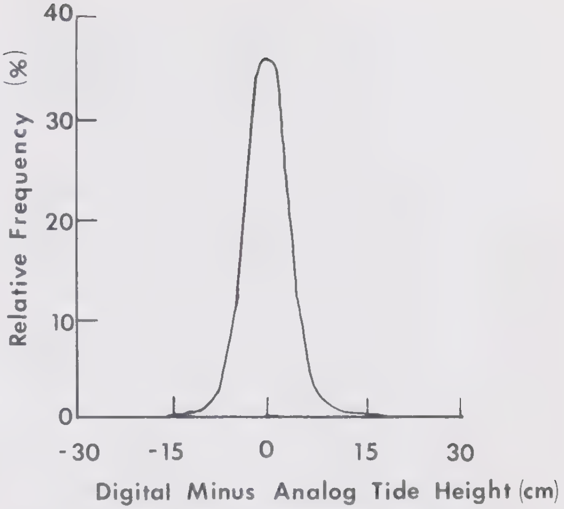

Figure 2.—Comparison of hourly tide measurements in Monterey Bay, Calif., from digital and analog gages for calendar year 1974. Total number of observations was 107,954.

To determine trends in the Monterey sea level record during the period 1963 through 1978, a least-squares linear fit was made to the time-series on monthly mean values. The fit showed a relative rise in sea level of about 0.01 cm/yr. The variability in sea level due to oceanographic and meteorological processes greatly exceeds this trend and thus the effects of long term trends were neglected in this study.

Of the long-period astronomic tides, the nodal tidal constituent, which results from the changing declination of the moon over a period of 18.61 yr, has the greatest amplitude. The theoretical amplitude of this constituent varies with latitude, with maximum effects at the Equator and the poles and minimum effects near lat. 35°N and 35°S (Lisitzin 1974). A second significant long period constituent, the annual solar tide, has an amplitude approximately one-fifth of the nodal tide component. The effects of this tidal constituent vary with latitude in a manner similar to that of the nodal tide. Monterey, located near lat. 36°N, is in a region where the ranges of both of these long period tides are about 1 cm, so these effects were neglected in this study.

Ocean and Atmospheric Data

The atmospheric pressure and wind data used in this study were derived from 6-h synoptic surface pressure fields prepared by Fleet Numerical Oceanography Center (FNOC). The pressure fields, interpolated onto a grid with a mesh length of 3° latitude and longitude, were used to compute geostrophic winds, from which wind stress, Ekman transport, and Sverdrup transport estimates were calculated at a deep water site approximately 14 km west of Monterey (Fig. 1). A description of the methods and computations used in these calculations is given by Bakun (1975). Briefly, the geostrophic wind was computed for the point lat. 36.6°N, long. 122.1°W and an estimate of the wind near the sea surface was made by rotating the geostrophic wind vector 15° to the left and reducing its magnitude by

30%. The surface wind stress was computed and the wind stress vector was resolved into north-south (meridional or alongcoast) and east-west (zonal or crosscoast) components. Ekman transport was computed and offshore-onshore transport was determined by resolving the vector component perpendicular to the general trend of the coastline. Sverdrup transport was calculated as described by Nelson (1977).

The surface temperature and salinity data were obtained from samples taken daily at Hopkins Marine Station of Stanford University during the period January 1963 to May 1975. SST data from June 1975 to December 1978 were taken at the Monterey tide station by NPS personnel. Salinity data from Hopkins Marine Station are not available later than May 1975.

To examine the relationship between sea level and dynamic height, a series of hydrographic cast data were assembled for a station located in mid-Monterey Bay, about 19 km northwest of the tide station (Fig. 1). This hydrographic station is located near the mouth of the Monterey submarine canyon where the water depth is over 900 m. The hydrographic cast data were taken semimonthly by the Hopkins Marine Station during 1963-73. Sampling during the first years of the program was limited to the upper 50 m of the water column but in 1968 the sampling depth was increased to over 500 m.[3] Sampling was discontinued by Hopkins in December 1973 and was resumed by Moss Landing Marine Laboratory from July 1974 to June 1978.[4]

The Hopkins and Moss Landing hydrographic data were keypunched and profiles of temperature and salinity and temperature-salinity curves were plotted for each station. Using these plots, obvious errors in the data were eliminated.

The time series of hydrographic stations had a gap in early 1974 between the end of Hopkins sampling and the beginning of Moss Landing sampling. Several expendable bathythermograph (XBT) drops taken during this period by NPS are available for the mid-bay location. To be able to utilize these XBT data, it was necessary to estimate a salinity value for each temperature value. A density value was calculated for each pair of temperature-salinity observations in the hydrographic cast data and correlation analysis was made. Density was found to be better correlated with temperature ($r = 0.98$) than was salinity with temperature ($r = 0.96$). Thus a density value was computed for each temperature in the XBT profiles and then a companion salinity value was calculated for each temperature and density pair. This procedure also allowed estimation of salinity for some of the hydrographic casts where temperature but not salinity values were recorded. The hydrographic data were then checked for density instabilities and finally, dynamic height was calculated for each profile for the 0/200, 0/400, and 200/400 db (decabars) levels. The depth of maximum calculation was limited by the XBT profiles which extended to only 460 m. The final time series contained 202 profiles to at least 400 m in the 10-yr period April 1968 to June 1978.

Monthly means and anomalies of sea level, and of the ocean and atmospheric data described in the above sections, are presented graphically and in tabular form in Appendix B.

SEA LEVEL AT MONTEREY

Although the time series of hourly sea levels contains much valuable information on the occurrence, amplitude, and duration of anomalous short period sea level fluctuations, it was decided for this study to concentrate on variations of sea level of monthly period and longer and on their atmospheric and oceanographic causes. Weekly and 6-h sea level data are discussed but in a more limited way as are the statistical characteristics of hourly deviations from the predicted sea level. Readers interested in short period fluctuations are referred to Maixner (1973) who examined Monterey sea level data during the year 1971.

Means and Variations

Hourly Sea Level.—To analyze nontidal sea level variations, which are small compared with the normal tide range in this area, the tidal signal must first be removed. Three methods for this are averaging, filtering, or subtracting predicted tides from the observed. The Tide Predictions Branch of the NOS performed a harmonic analysis of 365 d of hourly Monterey tide height values and isolated 37 harmonic constituents (Maixner 1973). Using the 20 constituents whose amplitudes were >0.61 cm, the NOS computed predicted hourly tide heights for the period of record, 1963 through 1976. Predicted hourly heights were then subtracted from the 13 yr of observed hourly heights to yield nonastronomic residuals. The frequency of occurrence of these sea level differences (observed minus predicted), which total nearly 108,000 values, approximates a normal or Gaussian distribution (Fig. 3). Of the observations, 94.5% lie within 15.2 cm (0.5 ft) of the predicted tide and 99.9% lie within 30.5 cm (1.0 ft). The maximum observed difference was 39.6 cm. The standard deviation of the differences was 8.7 cm, skewness -0.02, and kurtosis 3.2.

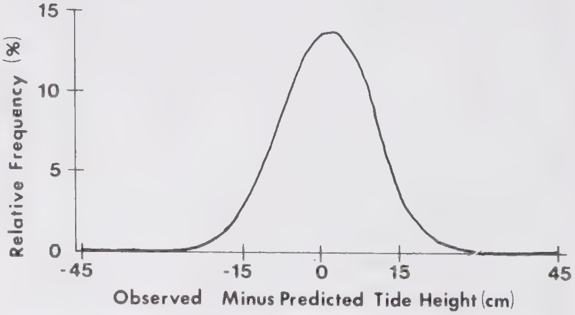

Figure 3—Frequency of occurrence of differences between observed and predicted hourly tide heights at Monterey, Calif., 1963-76.

The distribution of hourly differences describes nontidal sea level variations over a 13-yr period but gives no information about seasonal variations of the frequency distribution. Are distributions for winter months the same as those for summer? To define the seasonal change, curves were generated using data from 8,200 to 9,800 observations for each of the 12 mo of the year (Fig. 4). The frequency distribution of nontidal sea level fluctuations changes seasonally. In April, for example, 73% of the observed sea levels were lower than predicted, but in September, 81% of the observed data were greater than predicted. From March through May, observed sea levels tend to be lower than predicted sea levels, probably due to offshore Ekman transport, low water temperature, and atmospheric pressure effects as discussed later. From July through January, observed sea levels are higher than predicted due to atmospheric pressure and thermal expansion effects during summer and fall, and to onshore transport, pressure, and thermal effects during the Davidson Current period in December and January. It is not clear why these seasonal differences occur since one would expect seasonal effects to have been included in the harmonic constituents. Perhaps the differences occur because of variations in the frequency of occurrence of events in different years. Thus harmonics generated from measurements in only a single year may not be typical of other years.

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[3] Hopkins Marine Station. CalCOFI Hydrographic Data, collected on approximately bi-weekly cruises on Monterey Bay, California. Annual reports for years 1968 to 1973 (mineogr.). Hopkins Marine Station, Pacific Grove, CA 93950.

[4] Broenkow, W. W., S. R. Lasley, and G. C. Schrader. 1975. CalCOFI Hydrogrphic Data Report, Monterey Bay, July to December 1974. Tech. Publ. 75-1. Moss Landing Mar. Lab., Moss Landing, CA 95039.

Broenkow, W. W., S. R. Lasley, and G. C. Schrader. 1976. CalCOFI Hydrographic Data Report, Monterey Bay, January to December 1975. Tech. Publ. 76-1. Moss Landing Mar. Lab., Moss Landing, CA 95039.

Lasley, S. R. 1976. CalCOFI Hydrographic Data Report, Monterey Bay, January to December 1976. Tech. Publ. 77-1. Moss Landing Mar. Lab., Moss Landing, CA 95039.

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Chinburg, S. J. 1979. CalCOFI Hydrographic Data Report, Monterey Bay, January to June 1978. Tech. Publ. 79-1. Moss Landing Mar. Lab., Moss Landing, CA 95039.

The distributions of differences for winter months are wider and less peaked than those of summer months, indicating greater variability and larger nontidal events such as winter storms. In contrast, the distributions for July and August are narrow and more peaked.

Monthly Mean Sea Level.—Averaging of hourly sea level values over intervals of weeks to months removes the effects of the principal diurnal, semi-diurnal, and other short-term tidal components from the data to reduce the quantities of data to manageable size and to emphasize the longer time scales.

Monthly means of the hourly values were calculated for the period July 1963 through August 1976 and were updated for the period September 1976 through December 1978 with monthly mean values provided by the NOS. Figure 7 shows the long-term monthly means, standard deviations, and extremes of the monthly means of sea level at Monterey and other stations along the coast. Mean sea level at Monterey is lowest in April and highest in September, with a mean annual range of 13.6 cm. Variability is highest during winter months, with monthly standard deviations during winter being almost double those for summer. The range between maximum and minimum monthly values reaches a high of 21.0 cm in January and a low of 8.5 cm in August.

Anomalies of monthly sea level were calculated as differences between the monthly mean and the long-term mean for the same month. Calculation of anomalies in this manner removes the annual cycle from the data and allows examination of processes of nonannual periods. Monthly mean sea levels and their anomalies are shown in tabular and graphical form in Appendix B. In these figures extreme monthly sea level anomalies are shown to range from -10.8 cm in December 1975 to +10.7 cm in January 1978. Periods of anomalously high sea level occurred during 1969, 1972-73, 1976-77, and early 1978, and periods of anomalously low sea level occurred in 1964, 1970, 1971, 1973, 1975-76, and 1977.

To statistically define the persistence of anomalous periods, the autocorrelation function was used. This function describes the decay of the correlation coefficient of the data series with itself as the date series is time shifted relative to itself an increasing number of lag periods (months). The autocorrelation function of monthly Monterey sea level anomalies (Fig. 5) shows that sea level anomalies are correlated at the 5% level of significance for lags of up to 5 mo, indicating that anomalies persist over a period of several months. The autocorrelation function of the sea level series appears to decay exponentially for the first 8 mo or so, with significant negative autocorrelation coefficients occurring from lags of 11 to 18 and 23 to 26 mo.

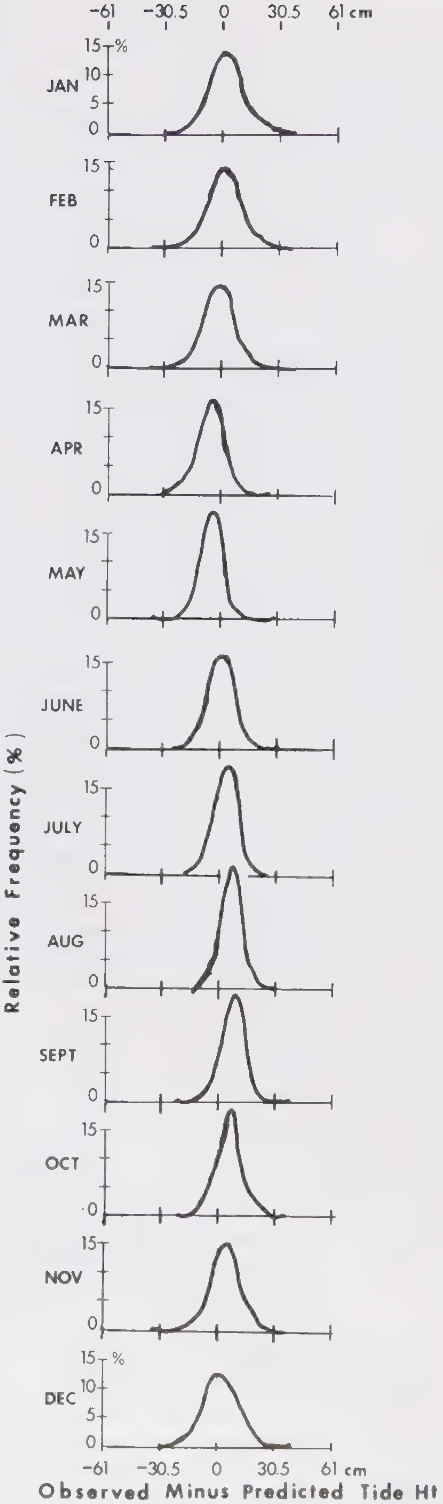


Figure 4.—Frequency of occurrence by month of differences between observed and predicted hourly tide heights at Monterey, Calif., 1963-76.

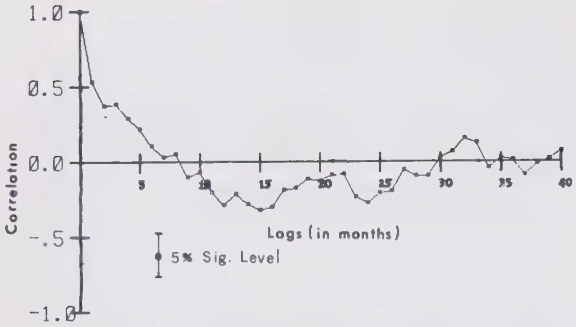


Figure 5.—Autocorrelation function for anomaly of monthly mean sea level at Monterey, Calif. The number of data points is 180 and the significance level is computed assuming a normal distribution of correlation coefficients.

Relation to Other Pacific Coast Tide Stations

We have seen that mean monthly sea level anomalies at Monterey tend to persist for up to 5 mo. The question naturally arises as to whether these anomalies are of local or regional geographic extent. To determine the spacial and temporal coherence between the monthly anomalies at Monterey and those observed at neighboring tide recording stations, monthly mean data were assembled for 15 tide stations along the Pacific coast ranging from Sitka, Alaska, to Callao, Peru (Fig. 6). These data were obtained from Klaus Wyrtki of the University of Hawaii and from the NOS. Stations selected for analysis were those having the best combination of the following characteristics: 1) representativeness of open ocean conditions, 2) long and continuous data record, 3) a constant tidal reference datum, and 4) suitable spacing between station locations along the coast. For each station, long-term monthly means were calculated from the available data for the period 1963 to 1978 and monthly sea level anomalies were derived (Fig. 7).

For stations north of Crescent City, frequent energetic winter storms cause the time series of anomalies to have only moderate persistence whereas stations south of San Francisco have much greater persistence of anomalies. Perhaps the most striking feature of the time series is the high visual correlation of anomalies along the coast (Bretschneider and McLain 1979; Enfield and Allen 1980). The periods of anomalously high sea level at Monterey during 1969, 1972-73, 1976-77, and 1978 were common to most stations where data are available. Similarly, the periods of anomalously low sea level seen at Monterey in 1964, 1970, 1971, 1973, 1975-76, and 1977 occurred at most of the other stations.

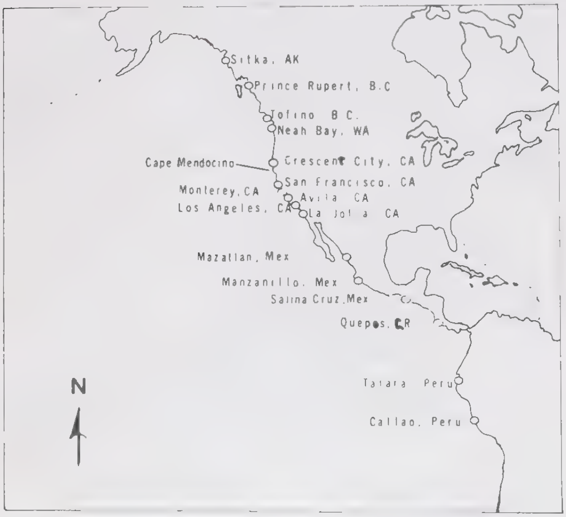


Figure 6.—Location of 15 tide stations along the west coasts of North and South America whose data were used in this study (see text).

Correlations of the monthly sea level anomalies between stations were calculated using the BMDP8D statistical program (Dixon 1975) and are tabulated in Table 1. The correlation of the selected tide stations relative to Monterey is shown graphically in Figure 8. Correlation of the Monterey anomalies is seen to be highest with San Francisco ($r = 0.85$) and lowest with Sitka ($r = 0.15$). Note also that the correlation coefficient drops off more rapidly with distance to the north of Monterey than to the south, due to the different space scales of the processes affecting sea level to the north and south.

Osmer and Huyer (1978) suggested the existence of two domains of coastal sea level fluctuations, with a boundary located south of San Francisco in winter and north of Crescent City in the spring and summer. The general location of their break-point is in agreement with the findings of Zee (1975), who suggested that sea level anomalies at stations from San Francisco southward to the Equator were related to nonseasonal vertical movements of the thermocline. That an oceanographic gradient or boundary may exist between northern and southern stations is further suggested by Nelson (1977) who showed that the area off northern California near Cape Mendocino is one of marked change in the seasonal surface wind stress field. The mean seasonal wind stress field over the coastal ocean south of Cape Mendocino is alongshore (southward) all year while the stress field north of Cape Mendocino is strongly onshore in winter and alongshore (southward) in summer.

The geographic coherence of sea level anomalies observed at Monterey with the neighboring tide stations along the coast was further examined in a time-distance domain. The monthly anomalies from the series of 15 coastal stations from Sitka, Alaska, to Callao, Peru, were plotted and contoured at 5 cm intervals for the period 1963 to 1974 (Fig. 9). Data for the years 1975-78 were not available for several of the stations so plots for these years are not included. The monthly anomalies have recognizable patterns which are coherent in both time and space. For example, large negative anomalies can be seen in January 1963 extending from Crescent City to Sitka and large positive anomalies in the same region occur in the subsequent fall and winter.

Anomalies of greater magnitude and stronger gradients in time and space occur northward of a boundary zone lying between Crescent City and Monterey, than to the south. Anomalous events north of this zone tend to occur simultaneously along the coast and persist for 1 or 2 mo. Anomaly magnitudes and gradients are also generally larger southward of a second, less well-defined boundary zone lying approximately between Manzanillo and Quepos. Between these boundary zones, gradients of the anomaly field are relatively weak. Southward of the zone between Crescent City and Monterey, sea level anomalies are of relatively long duration, as was noted earlier.

A particularly interesting event is the anomalously high sea level during the period October 1972 through February 1973 between Callao and San Francisco. This was a period of strong El Niño activity in the eastern tropical Pacific. During El Niño occurrences warm advection occurs into the eastern tropical Pacific Ocean and high SST's are observed. Sea level rapidly rises in the eastern tropical Pacific and falls slowly in the western Pacific (Wyrtki 1977). A peak sea level anomaly

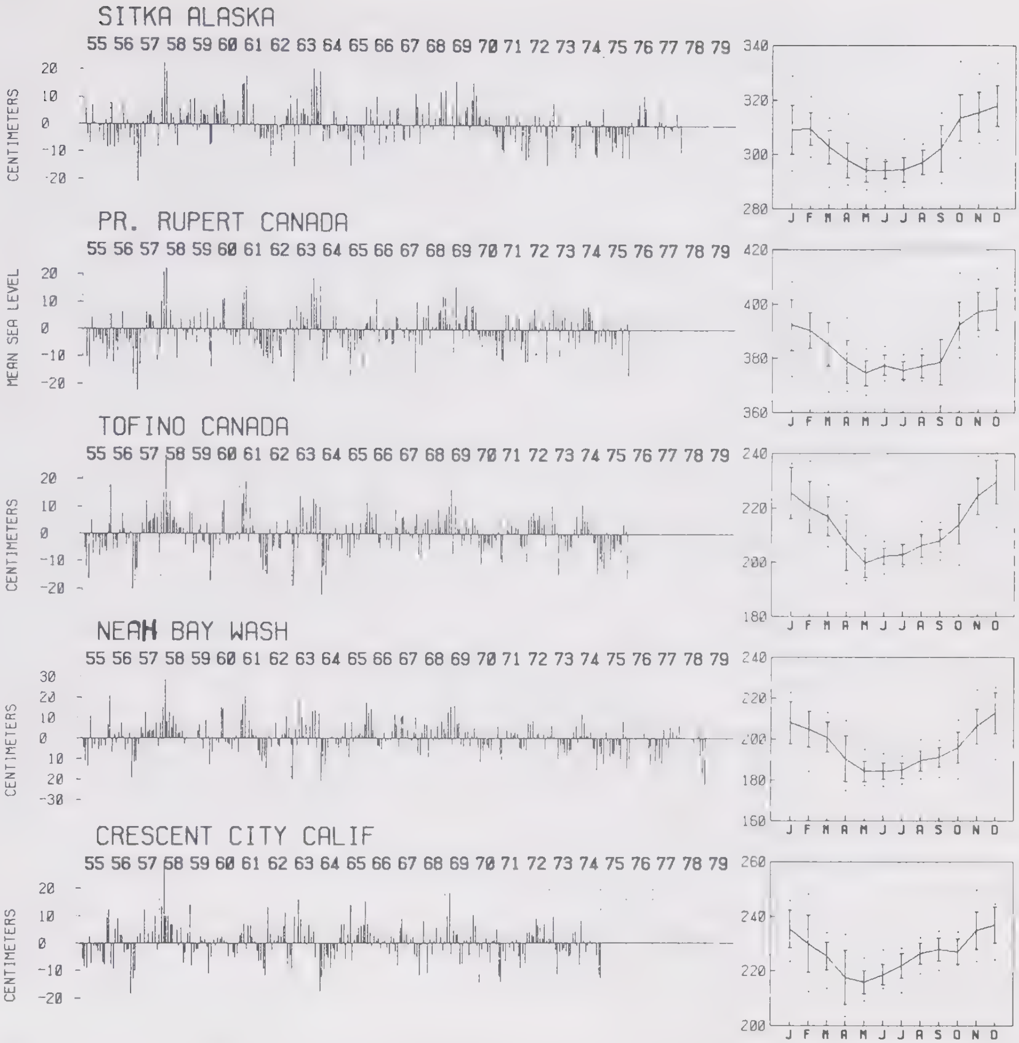


Figure 7.—Time series of monthly sea level anomalies for selected west coast tide stations. Inserts show mean annual cycle with standard deviations as vertical bars and monthly extremes as dots.

of 25 cm occurred at Manzanillo in December 1972, where the occurrence of high sea levels preceeded those observed at more northern stations by a month or more. At Monterey, sea levels were higher than average during the winter of 1972-73 (see also Fig. 7). During the El Niño period (see time-series plots in Appendix B), atmospheric pressures at Monterey were less than average and wind stress was negligible except during February 1973 when anomalous southerly winds resulted in onshore transport of surface waters and downwelling.

The strong alongcoast correlation of monthly sea level anomalies shows that sea level changes at Monterey are related to large-scale influences rather than to strictly local events. Table 1 shows that the anomalies at Monterey are correlated, at the 5% level of significance, with anomalies recorded at stations from Prince Rupert, Canada, to Callao, Peru, but are more closely related to events affecting sea levels in the group of stations from Crescent City to Quepos, Costa Rica. Processes producing the El Niño phenomenon in the eastern tropical Pacific also apparently affect sea level at Monterey. Recent theories (e.g., McCreary 1976) predict a deepening of the thermocline associated with the El Niño, which propagates northward along the coast as a Kelvin wave, and that northward geostrophic currents are produced behind the Kelvin wave fronts. Such currents cause changes in the cross shelf sea surface slope and northward advection of warm water. Both processes would cause anomalous increases in sea level at stations along the coast.

CAUSES OF SEA LEVEL VARIATIONS AT MONTEREY

The effects on sea level of changes in atmospheric pressure, changes in sea surface slopes due to changes in alongcoast currents, and changes in average density of the water column are all interrelated. A change in the distribution of atmospheric pressure over the ocean surface will generally change the horizontal gradient of pressure, resulting in a change in the geostrophic and other wind compo-

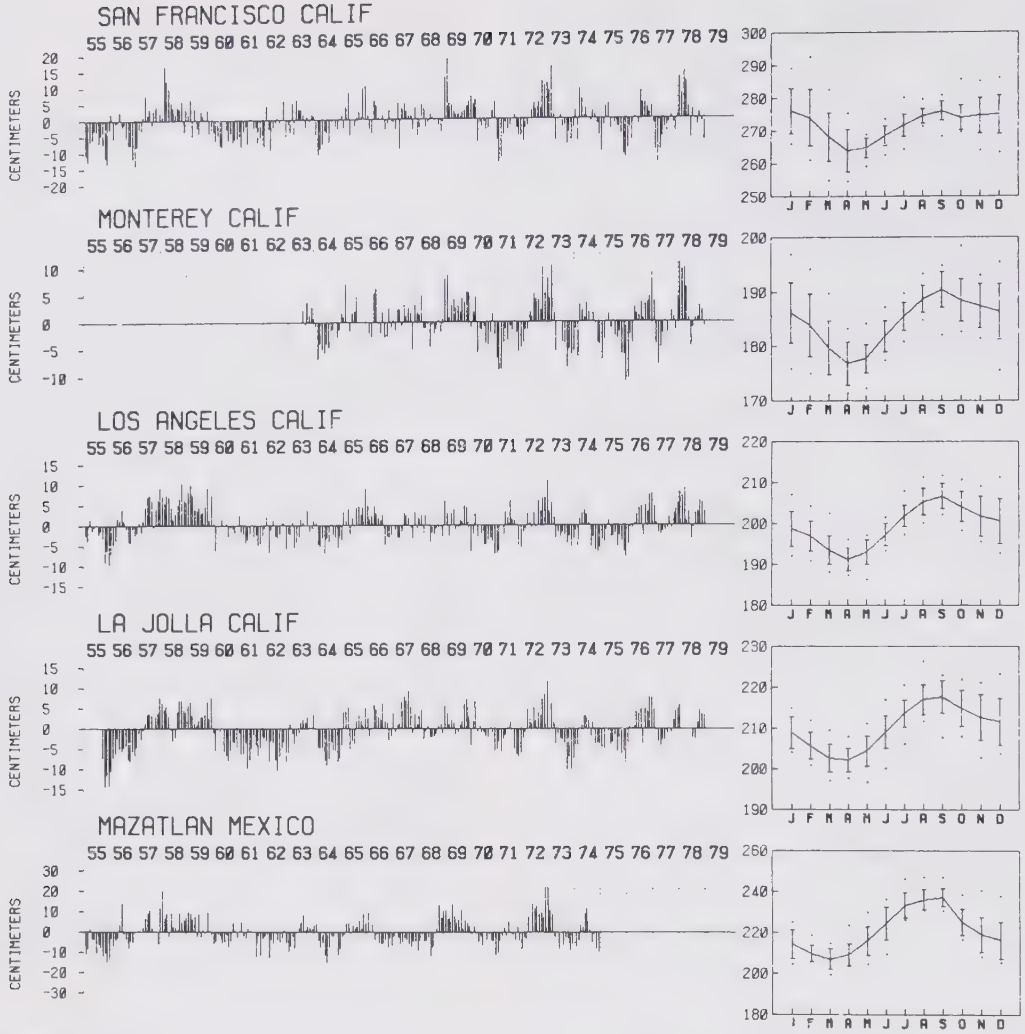


Figure 7.—*Continued.*

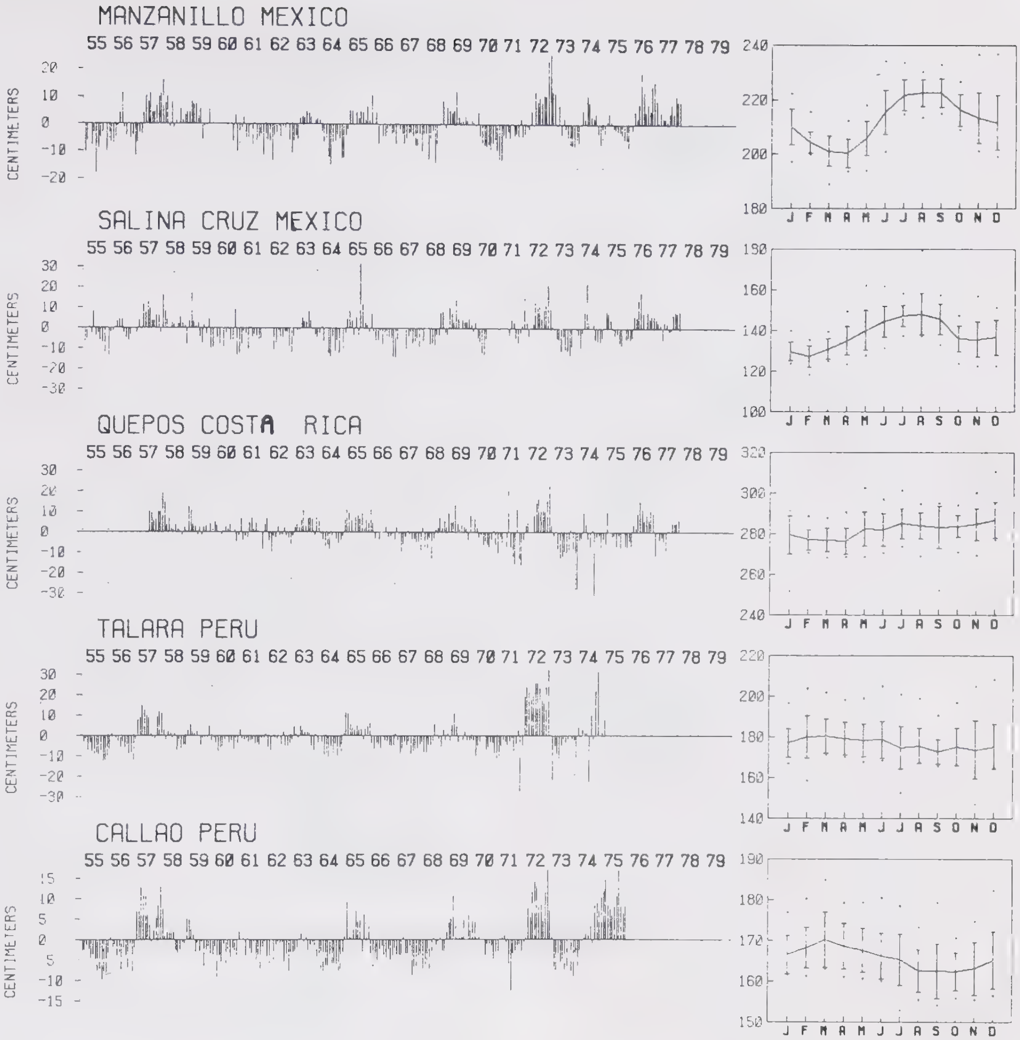
nents, and thus in wind stress. A change in wind stress will change the wind-driven current, redistribute the mass, and change the average density of the water column. Wind stress changes also alter wind-induced set-up or set-down against the coast. All of these processes combine with effects of a northward propagating wave from the tropics to affect sea level at Monterey.

Records of SST and salinity changes reflect changes in oceanographic conditions at the sea surface and may also be indicative of changes in the subsurface density distribution. Dynamic height calculations, however, provide a direct measure of the subsurface density field and its changes, and therefore reflect large scale changes in ocean circulation. If a strong relationship between sea level and dynamic height were found, it would allow use of inexpensive tide gage data to monitor changes in coastal circulation. The time series of frequent hydrographic stations taken in mid-Monterey Bay during 1968 to 1978 provide a unique opportunity to test for such a relation.

Correlation, regression, and spectral analysis techniques were used to study the causes of the sea level variations. These variations occur on various time scales and the analysis techniques used were chosen as appropriate for the time scale and character of the data to be analyzed. Thus, this section is organized generally by time-sampling and specifically by analysis procedures.

Correlation Analysis

Long term monthly means and anomalies for the period 1963-78 were calculated for the following oceanic and atmospheric variables: surface atmospheric pressure, meridional component of wind stress, zonal wind stress, offshore component of Ekman transport, Sverdrup transport, salinity, SST, and 0/400 db dynamic height. The data are presented numerically and graphically in Appendix B. Correlations between these variables and the monthly sea level anomalies at Monterey were calculated using the BMDP8D statistical program (Dixon 1975) and the results are given in Table 2. The correlation analysis measures the strength of the linear relationship between two random variables. However, the variables dealt with here are not random and may be mutually dependent on some third but unmeasured variable. Thus care must be used in interpretation of the statistical results. In



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the following paragraphs each variable will be treated in turn and the results of the correlation analysis will be discussed.

The effect on sea level of changes in atmospheric pressure over the oceans has been examined by a number of authors (Patullo et al. 1955; Saur 1962; Roden 1960). An increase (decrease) in atmospheric pressure results in a decrease (increase) in sea level. The pressure effect can be quite large in some areas, particularly in the Gulf of Alaska where winter storms are intense or along the Gulf or Atlantic coasts of the United States during the passage of hurricanes.

The isostatic contribution of atmospheric pressure variations to variations in sea level is computed from the hydrostatic equation $\Delta p = -\rho g \Delta h$ where Δp is the change in atmospheric pressure in millibars (mb), ρ is the density of water in g/cm^3, g is the acceleration of gravity in cm/s^2, and Δh is the change in sea level in centimeters. Applying this equation to seawater of density 1.025 g/cm^3 and using 980.7 cm/s^2 as the acceleration of gravity, we find that an increase in atmospheric pressure of 1 mb will result in a 0.995 cm depression of sea level.

The annual seasonal range of monthly mean atmospheric pressure at Monterey during the period 1963-78 was 7.3 mb, but pressure changes several times greater than this are not uncommon during the passage of intense winter storms. Thus, the effect of atmospheric pressure is expected to account for a significant portion of sea level variability near Monterey.

Maixner (1973) examined hourly data recorded from the Monterey tide gage during the year 1971 and concluded that sea level responds rapidly (within several hours) to pressure changes in an approximately hydrostatic manner. The coefficient of correlation between monthly mean sea level anomalies and pressure anomalies, based on 180 mo of simultaneous data from the period July 1963 through December 1978, was found in the present study to be -0.69 (Table 2). The relatively large negative correlation indicates a significant response of sea level to pressure.

It is desirable to remove the static effects of atmospheric pressure from the monthly sea level data so that the influence on sea level of other variables can be readily examined. To accomplish this, monthly

Table 1.—Intercorrelation of monthly mean sea level anomalies for selected west coast tide stations. Abbreviations refer to names of stations shown in Figure 6. Correlation coefficients enclosed in parentheses are not significant at the 5% level.

	CAL	TAL	QPO	SCZ	MAN	MZN	LJLA	LA	MTRY	SF	CC	NEA	TF	PR	SKA
CAL	1.00														
TAL	.71	1.00													
QPO	.49	.57	1.00												
SCZ	.50	.44	.55	1.00											
MAN	.54	.49	.56	.72	1.00										
MZN	.64	.43	.55	.68	.90	1.00									
LJLA	.22	.26	.43	.42	.56	.51	1.00								
LA	19	.27	.50	.48	.63	.63	.79	1.00							
MTRY	.23	.21	.43	.43	.53	.56	.75	.75	1.00						
SF	.25	.17	.36	.31	41	.49	.57	.58	.84	1.00					
CC	.24	(.13)	.31	.33	.33	.37	.35	.38	.62	.67	1.00				
NEA	(.00)	(.05)	.26	.23	.21	.36	.15	.21	.32	.43	.75	1.00			
TF	(.02)	(.04)	.24	.26	.32	.41	.27	.36	.40	.47	.76	.94	1.00		
PR	(.03)	(.00)	.16	(.08)	.28	.37	.16	.24	.21	.27	.34	.67	.73	1.00	
SKA	(-.10)	(-.10)	.21	(.01)	(.12)	.22	.17	.15	(.15)	.17	.20	.49	.55	.81	1.00

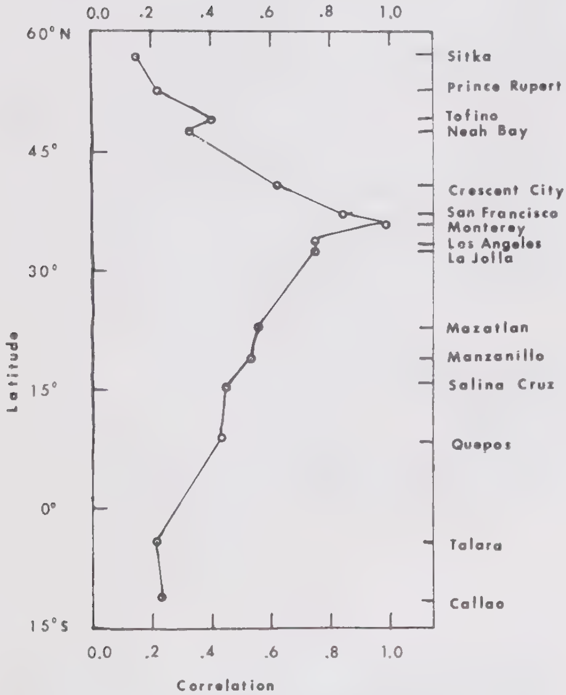


Figure 8.—Correlation of monthly sea level anomalies at selected west coast tide stations relative to Monterey, Calif.

mean sea levels were adjusted for monthly pressure effects by increasing (decreasing) sea level 1.00 cm for every 1.00 mb increase (decrease) of atmospheric pressure. The use of the more accurate value of 0.995 cm/mb was not warranted in this study. The magnitude of the pressure correction was determined by subtracting the long term mean pressure for the period January 1963 through December 1978 (1,016.85 mb) from the monthly mean atmospheric pressures. This method removes the effects of seasonal and interannual pressure changes. Mean monthly sea levels and sea level anomalies from which the hydrostatic effect associated with monthly pressure anomalies have been removed are referred to in this paper as adjusted sea levels.

In general, the effect of atmospheric pressure on sea level is small compared with the observed departures of sea level. In most months the pressure correction is opposite in sign to the sea level anomaly and reduces the variability of the sea level data. The effect of the static pressure correction on the seasonal sea level is to reduce the range of the monthly values, and to a lesser extent the seasonal range, but also to shift the month of occurrence of highest sea level from September to December. Pressure effects account for a portion of the sea level variability but significant nonbarometric residuals remain, indicating the effects of dynamic as well as static processes.

The effects of wind stress on sea level are two fold 1) the direct elevation or depression of water by winds normal to the coast and 2) the sea surface slopes created by offshore or onshore Ekman transport produced by winds parallel to the coast. The direct piling up of water against the shore is commonly observed along coasts with wide, shallow continental shelves or long, narrow embayments. The magnitude of this effect is dependent on basin configuration, surface wind velocity, depth of water, and the time scales considered. The continental shelf in the Monterey area is quite narrow with deep water located close inshore so that the effects of wind set-up are small. Defant (1961) showed, for example, that a constant 10 m/s wind blowing over a basin 50 m deep would produce a sea surface slope of 6.6 cm/100 km. The 50 m contour near Monterey is <1.6 km offshore (Fig. 1), and the magnitude of direct piling of water by the wind is thus less than the range of error in tide measurements. In addition, monthly anomalies of zonal (east/west) wind stress were found not to be significantly correlated with monthly sea level anomalies at the 5% level of significance (Table 2). Accordingly, elevation or depression of sea level by cross shore wind stress is neglected in this analysis.

The second effect of wind stress is that of sea surface slopes produced by offshore or onshore Ekman transport due to winds parallel to the coast. According to conventional Ekman transport theory, net transport is directed 90° to the right of the wind in the Northern Hemisphere. In this study, offshore/onshore Ekman transport was found to be significantly correlated with sea level ($r = -0.42$ in Table 2). The inverse correlation indicates that offshore transport results in decreased sea level and onshore transport in increased sea level. Meridional wind stress is also significantly correlated with sea level ($r = 0.43$), as expected. Monthly anomalies of Sverdrup transport were found not to be significantly correlated with monthly sea level anomalies at the 5% level.

Sea surface temperature and surface salinity are both significantly correlated with monthly sea level anomalies (with correlation coefficients of 0.61 and -0.35). The signs of the correlations indicate that

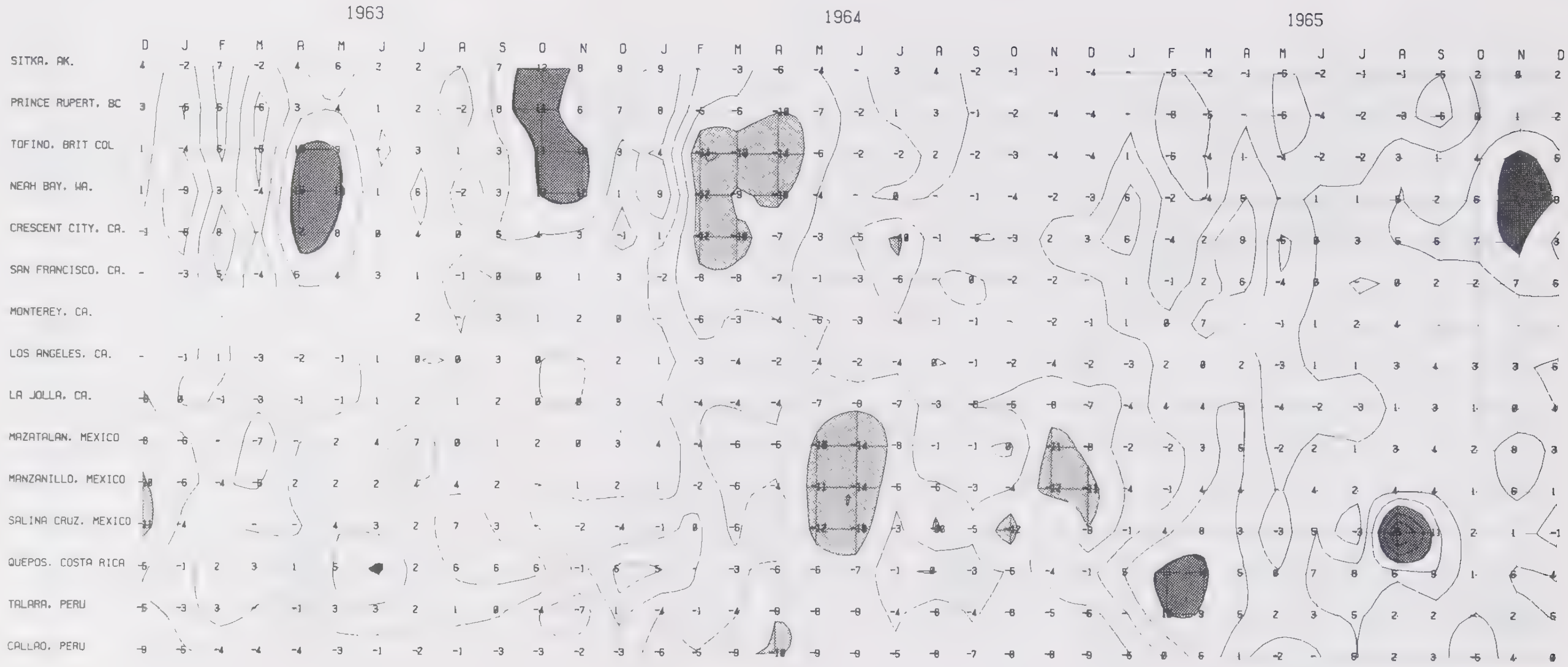
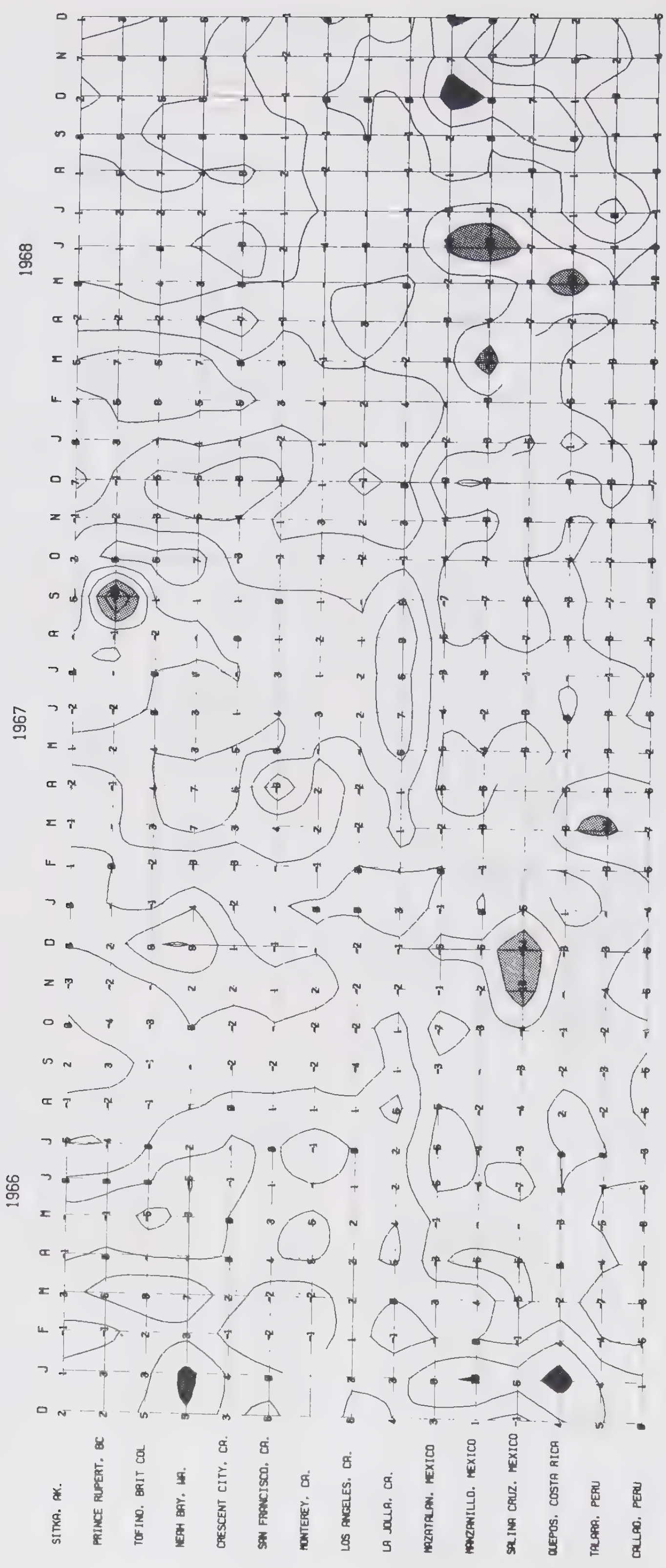


Figure 9.—Time-distance contour plot of monthly mean anomalies of sea level in centimeters from 1962-74 mean at selected west cost tide stations. The contour interval is 5 cm with areas greater than +10 cm shaded dark and areas less than -10 cm shaded light.



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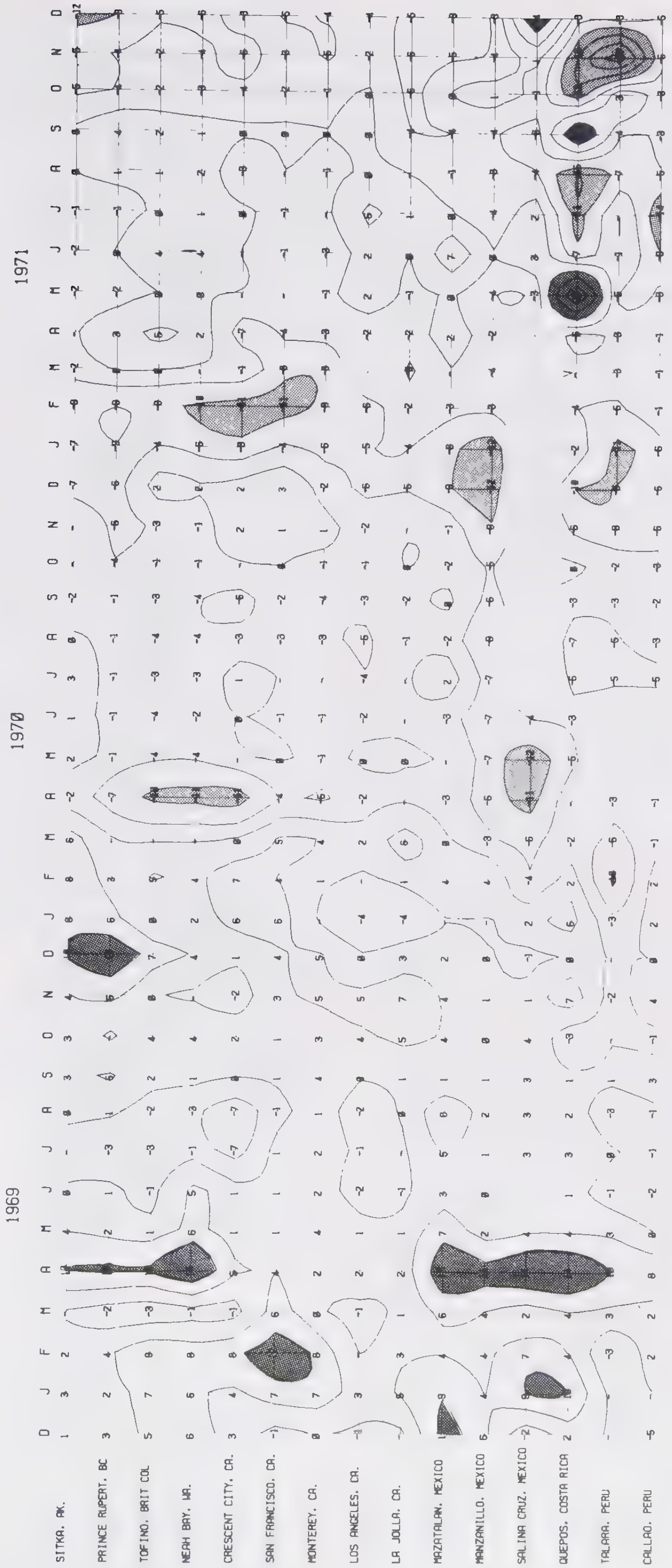

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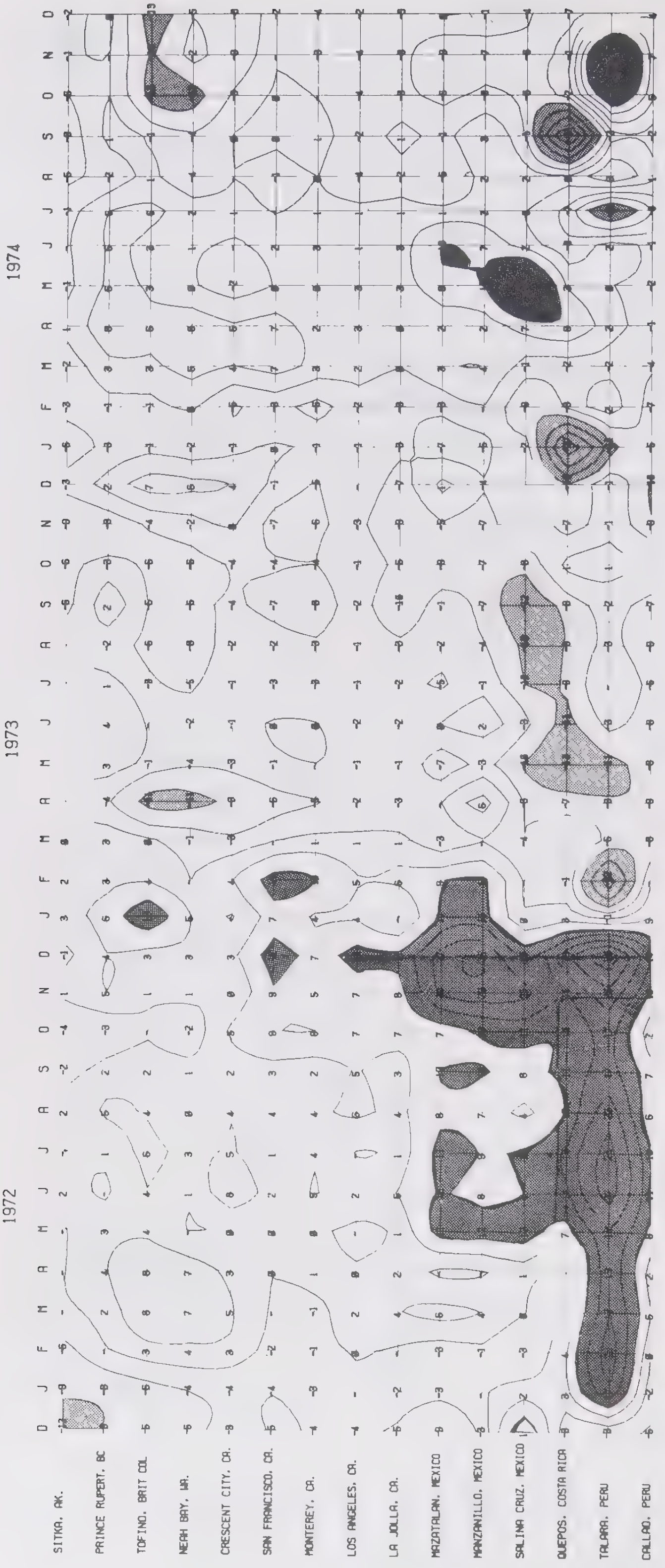

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Table 2.—Intercorrelation of monthly mean anomalies of sea level with various oceanic and atmospheric variables at Monterey, Calif. (see text). Correlation coefficients enclosed in parentheses are not significant at 5% level.

	SL	ADJ SL	PRESS	MERID WS	ZONAL WS	EKM TSPT	SVP TSPT	SAL	SST	DYN HT
SL	1.00									
ADJ SL	.96	1.00								
PRESS	-.70	-.46	1.00							
MERID WS	.43	.42	-.28	1.00						
ZONAL WS	(-.14)	-.18	(-.03)	-.48	1.00					
EKM TSPT	-.42	-.42	.26	-.99	.59	1.00				
SVP TSPT	(.01)	(.07)	-.18	-.33	.15	.32	1.00			
SAL	-.35	-.31	.29	-.31	(.07)	.30	.20	1.00		
SST	.61	.65	-.29	.38	-.17	-.37	(-.05)	-.37	1.00	
DYN HT	.79	.79	-.46	.25	(-.08)	-.25	(.00)	-.44	.65	1.00

increases in SST are associated with increased sea levels and increased salinities are associated with decreased sea levels. These relationships are consistent with basic considerations of seawater density changes.

Dynamic height (0/400 db) at the mid-Monterey hydrographic station was found to be strongly correlated with sea level fluctuations at Monterey. The correlation coefficient of 0/400 db dynamic height was 0.79 with Monterey sea level and was the highest of any of the variables tested. The higher correlation of sea level with dynamic height than with SST (r = 0.61) suggests that subsurface fluctuations are important in causing changes of both sea level and dynamic height at Monterey. A possible cause of such subsurface fluctuations is the northward propagating coastally trapped wave mentioned earlier. To examine this, sea level at Talara, Peru, was used as an index of El Niño conditions and was lagged 0 to 10 mo for correlation with sea level at Monterey. The correlation coefficient peaked at r = 0.37 at a lag of 6 mo. A wave propagating the approximately 6,300 km between Talara and Monterey in 6 mo would have a phase speed of about 34 km/d. This is somewhat lower than speeds reported by Enfield and Allen (1980) but not inconsistent with their results.

Regression Analysis

We have seen that the monthly anomalies of sea level at Monterey are significantly correlated with dynamic height, atmospheric pressure, SST, meridional wind stress, offshore Ekman transport, and surface salinity. To quantify these relationships, a multiple regression analysis was performed using the BMDP2R stepwise multiple regression program (Dixon 1975). Since fluctuations of meridional wind stress and offshore Ekman transport are closely related (r = 0.99 in Table 2), use of both variables in a regression would cause instabilities in the computation. Ekman transport was omitted from the regressions and only the meridional wind stress considered since the wind stress is the more fundamental variable.

The results of the regression analysis for the entire year, presented in Table 3 (Part A), show that dynamic height is the major predictor of sea level, with atmospheric pressure, SST, and meridional wind stress as second, third, and fourth predictors. The remaining variables explained only negligible portions of the variance and their coefficients are not included in the table. Together, the four major predictors explain over 76% of the variance of the monthly sea level anomalies with dynamic height alone explaining 62% of the variance. Considering that the sea level was recorded hourly in a consistent fashion while dynamic height was computed from observations taken at scattered times by several institutions using different methods, the strength of the relation seems very good.

Table 3.—Results of multiple regression analysis of sea level at Monterey, Calif., with various oceanic and atmospheric variables for entire year, Davidson Current, and upwelling periods. Data series are sea level (SL) in centimeters, atmospheric pressure (PRESS) in millibars, sea surface temperature (SST) in °C, meridional wind stress (MWS) in dynes/cm², and dynamic height (DYN HT) in centimeters.

Step	Variable	Explained variance	Increase in explained variance
A. Entire year (Jan.-Dec., 77 mo of data)			
1	DYN HT	.62	.62
2	PRESS	.70	.08
3	SST	.74	.04
4	MWS	.76	.02
Sea level = -0.057 + 0.470 DYN HT - 0.894 PRESS + 1.208 SST + 4.491 MWS			
B. Davidson Current period (Oct.-Feb., 31 mo of data)			
1	DYN HT	.76	.76
2	MWS	.82	.06
Sea level = -0.0653 + 0.732 DYN HT + 15.402 MWS			
C. Upwelling period (Apr.-Aug., 33 mo of data)			
1	DYN HT	.36	.36
2	MWS	.52	.16
3	PRESS	.60	.08
4	SST	.66	.06
Sea level = -0.108 - 0.935 PRESS + 0.256 DYN HT + 4.256 MWS + 1.271 SST			

The relationship between sea level and dynamic height was further examined in a seasonal sense. There is good agreement in both phase and amplitude of the long term monthly means of dynamic height and adjusted sea level (Fig. 10). The observed seasonal cycle for dynamic height is somewhat more variable than that of sea level, possibly as a result of limited sampling (there were only 12 or 13 stations per month during winter but up to 24 stations per month the rest of the year). The figure shows that both sea level and dynamic height near Monterey are highest in winter and lowest in spring.

Reid and Mantyla (1976), showed that south of lat. 40°N in the eastern North Pacific Ocean sea levels are typically highest in late summer and early fall and lowest in late winter as a result of annual solar heating. North of lat. 40°N, however, sea levels are highest in winter and lowest in summer; this pattern cannot be explained by the steric response to seasonal heating and cooling. Using Sturges' (1974) data from Neah Bay, Reid and Mantyla further demonstrated that maximum sea levels occur in winter when inshore northward flow is strongest and minimum sea levels occur during summer when flow is southward, thus relating seasonal changes in sea level to geostrophically balanced flow. Monterey lies at lat. 36°N and has a seasonal cycle that is intermediate between these regimes.

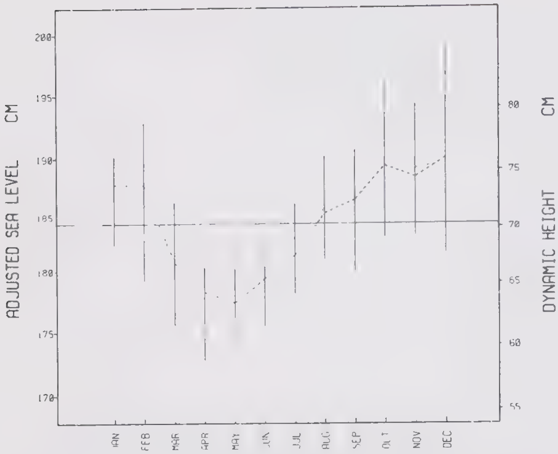

Figure 10.—Seasonal cycle of sea level and dynamic height near Monterey, Calif. Sea level data are for 1963-78 and shown as dotted line and dynamic height data are for 1968-77 and shown as dashed line. Ranges of monthly sea levels are shown by vertical bars.

Sea level and dynamic height are also in good agreement in a time series sense. Figure 11 shows the time series of weekly mean sea level, calculated from the hourly data, and individual dynamic height calculations relative to 200 and 400 db. The figure shows that both sea levels and dynamic heights were higher than normal during 1969–70, 1972–73, and 1976, which were periods of El Niño activity in the eastern tropical Pacific. Sea levels and dynamic heights were both also near or below normal during anti-El Niño periods. Because of the close agreement between seasonal cycles of sea level and dynamic height, and because of the high correlation of sea level at Monterey with that at adjacent stations, dynamic height and sea level variations may both reflect variations in the alongshore geostrophic current flow. To show this, one would have to show that fluctuations of sea level were correlated with fluctuations of slope of dynamic height normal to the coastline. Suitable data for this may be available but this was felt to be beyond the scope of this report.

The regression formula indicates that the response of sea level to changes in atmospheric pressure is -1.67 cm/mb whereas a purely hydrostatic response would be -1.00 cm/mb. This higher than theoretical pressure response coefficient is poorly understood but is possibly due to reinforcement of the local pressure effect by a larger scale, dynamic aspect of the atmospheric pressure systems themselves. Saur (1962) and Roden (1960) analyzed monthly tide data from stations to the north and south of Monterey and found similar larger than expected pressure response coefficients.

Because of the significant seasonal changes in the oceanic and atmospheric regimes near Monterey, we might expect to observe seasonal changes in the processes affecting sea level. To define these seasonal changes, the ocean and atmospheric variables were analyzed separately for the two major periods, the Davidson Current and the upwelling periods (Table 3).

Sea level changes during the Davidson Current period were analyzed using data from 5 mo, October through February, for the years 1963-78. The results of multiple regression analysis indicate that dynamic height and meridional wind stress are major predictors of sea level during this period, explaining 82% of the variance of monthly sea level anomalies. During this period, dynamic height and sea level are strongly correlated, $r = 0.87$.

The second period analyzed was centered during the upwelling period and covered 6 mo, April through August, during the years 1964-78. During this period, dynamic height remains the primary predictor but at weaker correlation, $r = 0.60$. Atmospheric pressure, SST, and meridional wind stress are secondary predictors and in total account for 66% of the variability of monthly sea level.

Thus, some seasonal change in the processes affecting sea level is indicated, with dynamic height accounting for most of the sea level variability in both the upwelling and Davidson Current periods. Meridional wind stress is also important during both periods but more so during the upwelling than Davidson Current period. Atmospheric pressure and SST explain an additional portion of the sea level variability during the upwelling period. The greater amount of explained variance in winter than summer suggests that conditions in winter are dominated by changes in the structure of the water column whereas upwelling in summer causes complicated effects on sea level.

Spectral Analysis

In the previous section, it was shown that most of the variance of monthly sea level anomalies can be explained by monthly anomalies of dynamic height, surface atmospheric pressure, SST, and meridional wind stress. However, important variations in these processes occur on time scales shorter than a month. To determine how the variance of sea level is distributed with frequency over time-periods of days to weeks, auto- and cross-spectra were calculated for 6-h observations of sea level, atmospheric pressure, and meridional wind stress. Spectra of dynamic height and SST were not computed because the required data were too sparse.

To prepare these data for spectral analysis, it was necessary to subsample the hourly sea level series at the 6-h period of the available surface atmospheric pressure and meridional wind stress data. Atmospheric pressure and meridional wind stress were calculated as described previously on a 6-h basis for the period 1 January 1967 through 31 August 1976 for a point approximately 14 km west of the Monterey tide station (Fig. 1). Hourly sea level data for the same time period were low-pass filtered to remove the diurnal, semidiurnal, and other short-term tidal components and were subsampled at 6-h intervals. A complete description of the low-pass filter used is given by Godin (1966). All data series were then detrended by subtracting their 30-d running mean to produce band-passed series. The response function for the 30-d running mean is shown in Figure 12.

Atmospheric pressure, wind stress, and sea level data (unadjusted for pressure effects) were analyzed during the winter storm season (1 November to 8 March) and the upwelling period (1 April to 8 August) for the years 1967-76. The definition of these periods is somewhat arbitrary but was based on visual interpretation of time series of sea level and wind stress and on the requirement that the number of data points used in the spectral analysis be a power of 2. Since the periods are normally 3-4 mo long, 512 data points (128 d) were used. A fast Fourier transform spectrum analysis with a triangular data window was used and the spectra were averaged for all available years. The frequency bandwidth is 0.04 cycles per day (cpd) and the number of degrees of freedom is 90 for the winter period and 100 for the upwelling period.

The spectral relationships between sea level and atmospheric pressure are discussed first. In the low frequency region, the winter period spectra (Fig. 13) are three to four times more energetic than the upwelling period spectra (Fig. 14), indicating the effects of intense winter storm events. The largest sea level and pressure fluctuations

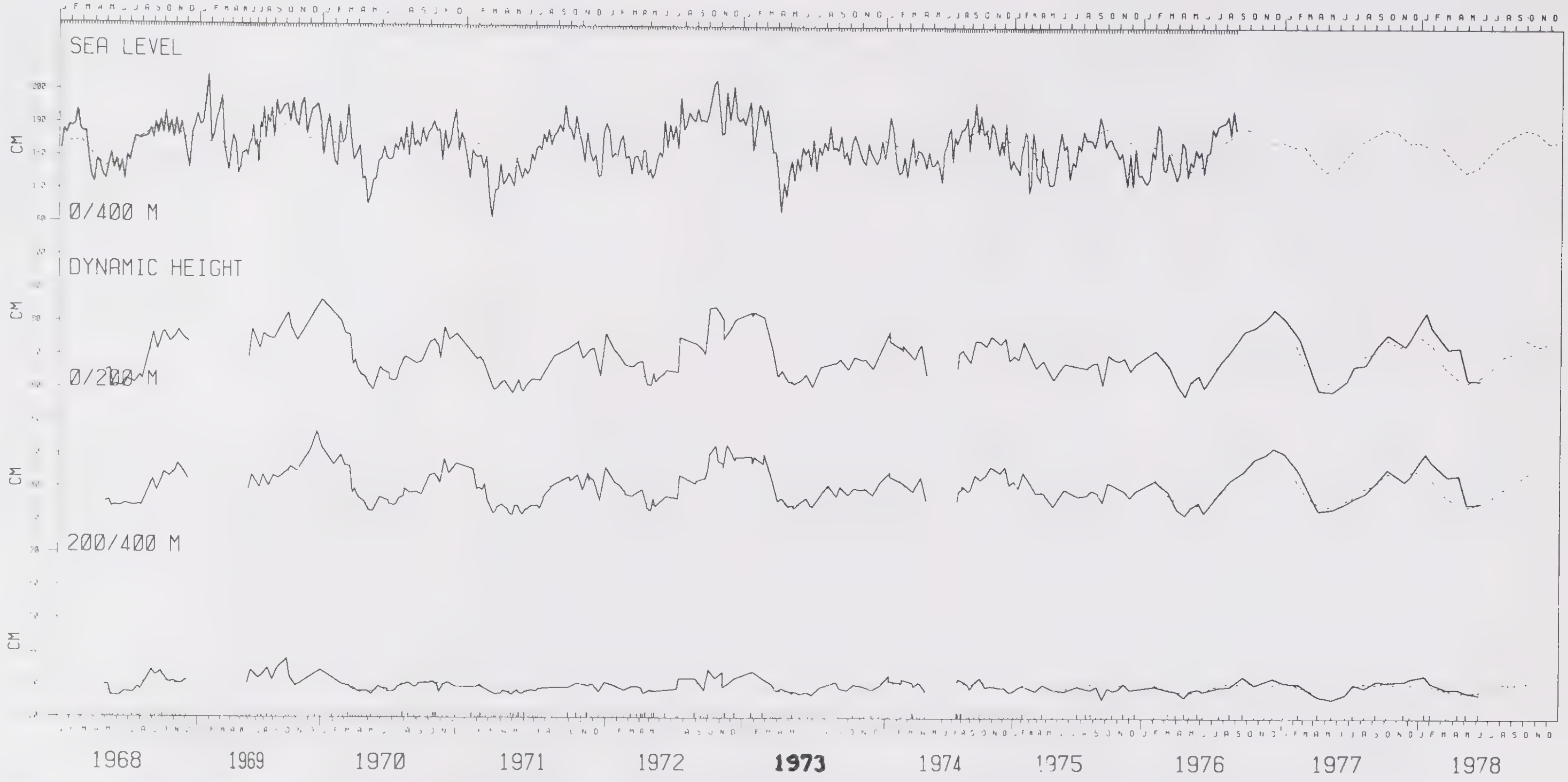

Figure 11.—Time series of weekly mean sea level at Monterey, Calif., and dynamic height computed from frequent hydrographic stations in mid-Monterey Bay. The mean annual cycles are shown as dotted lines.

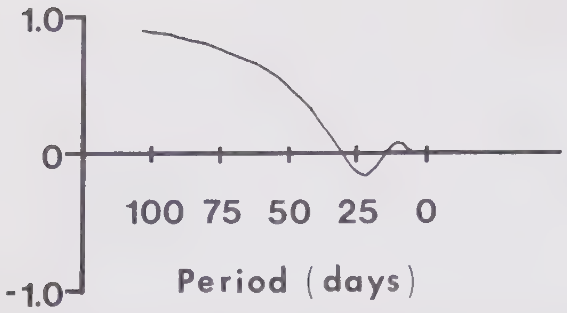

Figure 12.—Amplitude response function for the 30-d running mean filter used to low pass filter hourly sea level data from Monterey, Calif.

occurred in the 0.04-0.08 cpd frequency band (24-12 d). This peak was present in all series and was significant at the 95% confidence level for pressure but not for sea level. Fluctuations of longer period than this peak appear to be more important for sea level than for pressure. The filters used in the analysis had been designed to isolate variations with periods 2-10 d (0.5-0.2 cpd) but did not reveal any significant spectral peaks in that region.

The coherence (squared) between sea level and atmospheric pressure was found to be significant and independent of frequency in the upwelling period (Fig. 14), but in the winter period (Fig. 13), decreased in magnitude at frequencies greater than 0.5 cpd (<2d). The nearly constant 180° phase angle between the two series reflects the inverse response between atmospheric pressure and sea level as expected from the hydrostatic equation.

In order to better examine the relationship of wind stress and sea level, the low-passed 6-h sea level series was adjusted for atmospheric pressure effects and detrended using the 30-d running mean filter described previously. Auto- and cross-spectra were then calculated for the 6-h adjusted sea level and meridional wind stress series (Figs. 15, 16). Like the atmospheric pressure and unadjusted sea level series, meridional wind stress had a concentration of energy at low frequencies with large variations occurring in the 0.04-0.08 cpd frequency band, and the winter season power spectra contained more energy than that of the upwelling season. Coherence between adjusted sea level and meridional wind stress is generally low. The phase angles provide little information because of the low coherence.

SUMMARY

Analysis of 13 yr of hourly sea levels indicates that nontidal sea level variations are small compared with the normal tide range in the area. The largest nontidal deviation observed was 39.6 cm. A seasonal change revealed by monthly frequency distributions of hourly nontidal sea level variations was found, with observed sea levels being generally less than the predicted during March through May and greater than the predicted from July through January.

Monthly sea level anomalies at Monterey are correlated with anomalies at tide stations from Prince Rupert, Canada, to Callao, Peru, but are most closely related to events affecting sea levels in the group of stations from Crescent City, Calif., to Quepos, Costa Rica. Processes producing the El Niño phenomenon in the eastern tropical Pacific affect sea level at Monterey with a lag of about 6 mo.

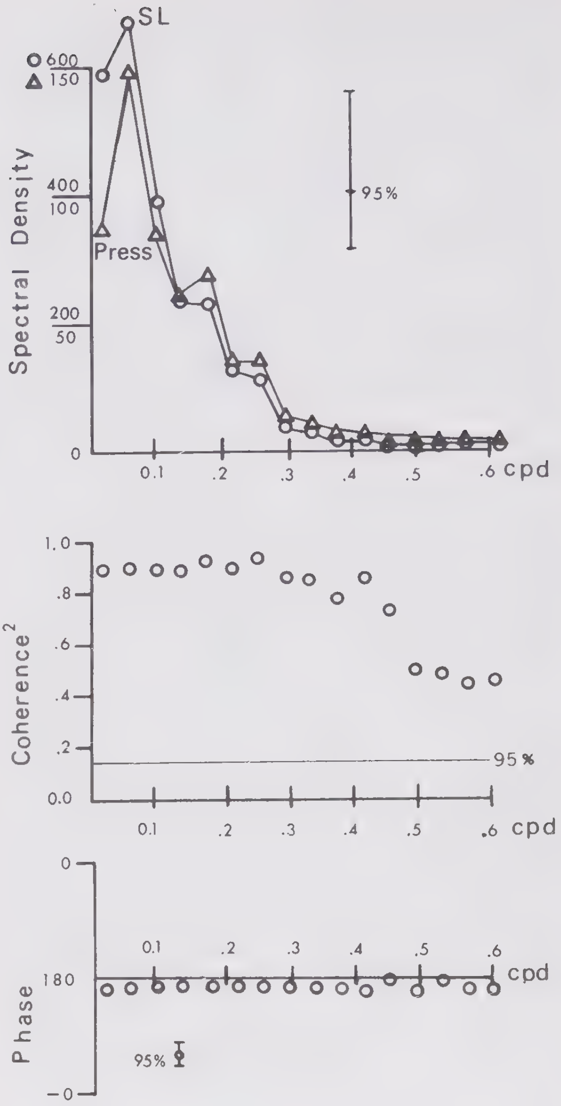

Figure 13.—Spectral plots of 6-h atmospheric pressure (Press) and unadjusted sea level (SL) for the winter period (df = 90) at Monterey, Calif. The horizontal axes are frequency in cycles per day (cpd). The upper plot shows spectral density of pressure (in mb²/cpd) and sea level (in cm²/cpd); the middle plot shows the squared coherence of the two series; and the lower plot shows the phase.

Multiple regression analysis indicates that monthly anomalies of dynamic height and meridional wind stress account for most of the monthly sea level variability at Monterey during both the Davidson Current and upwelling seasons. Atmospheric pressure and SST account for an additional portion of sea level variability during the upwelling season.

There is good agreement between the behavior of sea level and dynamic height in both a seasonal sense and in interyear variability. The close agreement between sea level and dynamic height, and the high correlation of sea level at Monterey with that at adjacent tide sta-

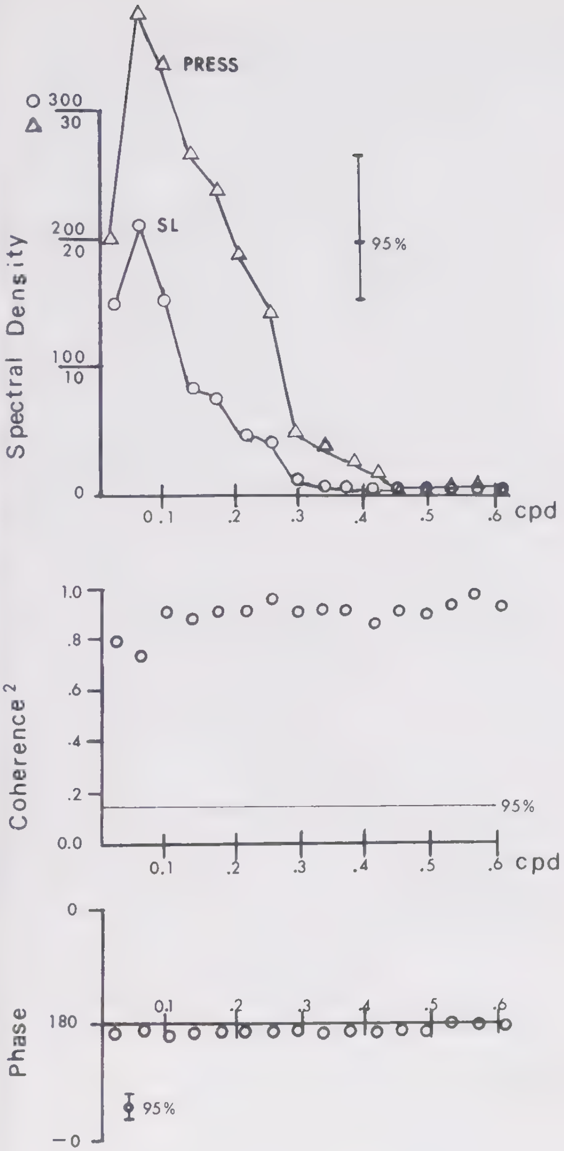

Figure 14.—Spectral plots of 6-h atmospheric pressure (Press) and unadjusted sea level (SL) for the upwelling period (df = 100) at Monterey, Calif. The horizontal axes are frequency in cycles per day (cpd). The upper plot shows spectral density of pressure (in mb²/cpd) and sea level (in cm²/cpd); the middle plot shows the squared coherence of the two series; and the lower plot shows the phase.

tions along the coast are both thought to result from variations in coastal current flow.

Analysis of 6-h sea level and atmospheric pressure observations shows that the power spectra in the winter season are more energetic than those of the upwelling season, and that most of the energy occurs at low frequencies (periods longer than 12 d). Coherence between sea level and atmospheric pressure is significant and independent of frequency. This and a nearly constant 180° phase relationship between these 6-h data sets reflects the inverse response between sea level and atmospheric pressure expected from the hydrostatic relationship. The power spectra for 6-h meridional wind stress also show a concentration of energy at low frequencies and are most energetic in winter; however, coherence between the local wind stress and sea level is generally low.

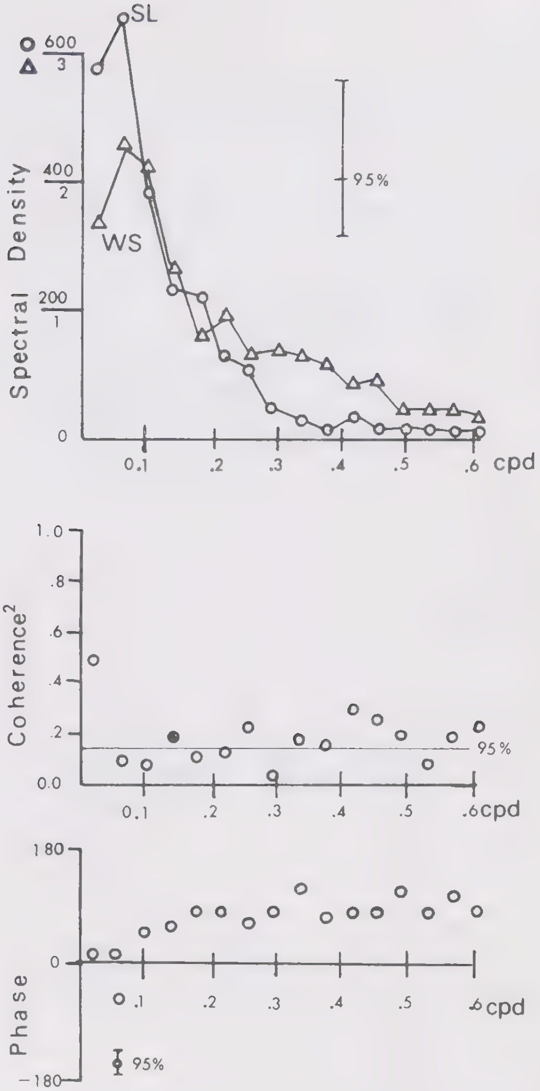

Figure 15.—Spectral plots of 6-h meridional wind stress (WS) and adjusted sea level (SL) for the winter period (df = 90) at Monterey, Calif. The horizontal axes are frequency in cycles per day (cpd). The upper plot shows spectral density of wind stress (in (dynes/cm²)²/cpd) and sea level (in cm²/cpd); the middle plot shows the squared coherence of the two series; and the lower plot shows the phase.

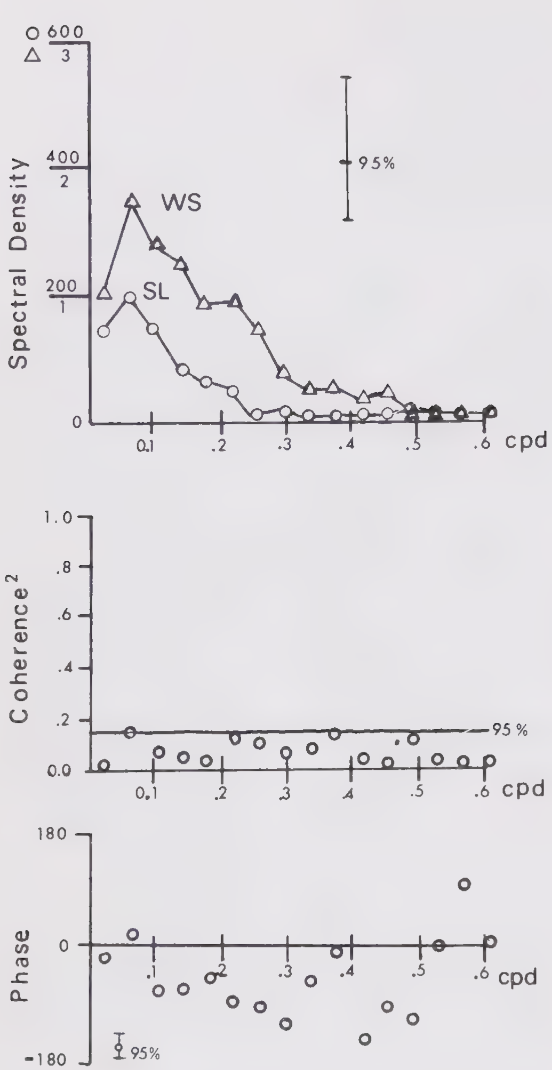

Figure 16.—Spectral plot of 6-h meridional wind stress (WS) and adjusted sea level (SL) for the upwelling period (df = 100) at Monterey, Calif. The horizontal axes are frequency in cycles per day (cpd). The upper plot shows spectral density of wind stress (in (dynes/cm²)²/cpd) and sea level (in cm²/cpd); the middle plot shows the squared coherence of the two series; and the lower plot shows the phase.

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APPENDIX A.—MISSING HOURLY SEA LEVEL DATA

The dates and times of missing hourly sea level observations at Monterey, Calif., are listed below. The data series began 21 July 1963 and ended 31 August 1976.

1963
25 Aug. 12AM-4 Sept. 11PM
28 Sept. 4AM-3 Oct. 6PM
16 Oct. 9AM-21 Oct. 11AM

1964
28 Mar. 12AM-30 Mar. 7PM

1965
1 Apr. 12AM-1 May 9AM
1 Sept. 12AM-31 Dec. 11PM

1966
1 Jan. 12AM-3 Feb. 3PM

1969
20 Sept. 12PM-23 Sept. 3PM

1970
6 Oct. 10PM-8 Oct. 3PM

1971
20 Jan. 7PM-23 Jan. 2PM

1975
14 Feb. 1PM-18 Feb. 3PM
22 Oct. 2AM-28 Oct. 11PM
7 Nov. 1AM-19 Nov. 11PM

1976
25 May 1AM-26 May 11PM

APPENDIX B.—MONTHLY MEAN OCEANIC AND ATMOSPHERIC OBSERVATIONS

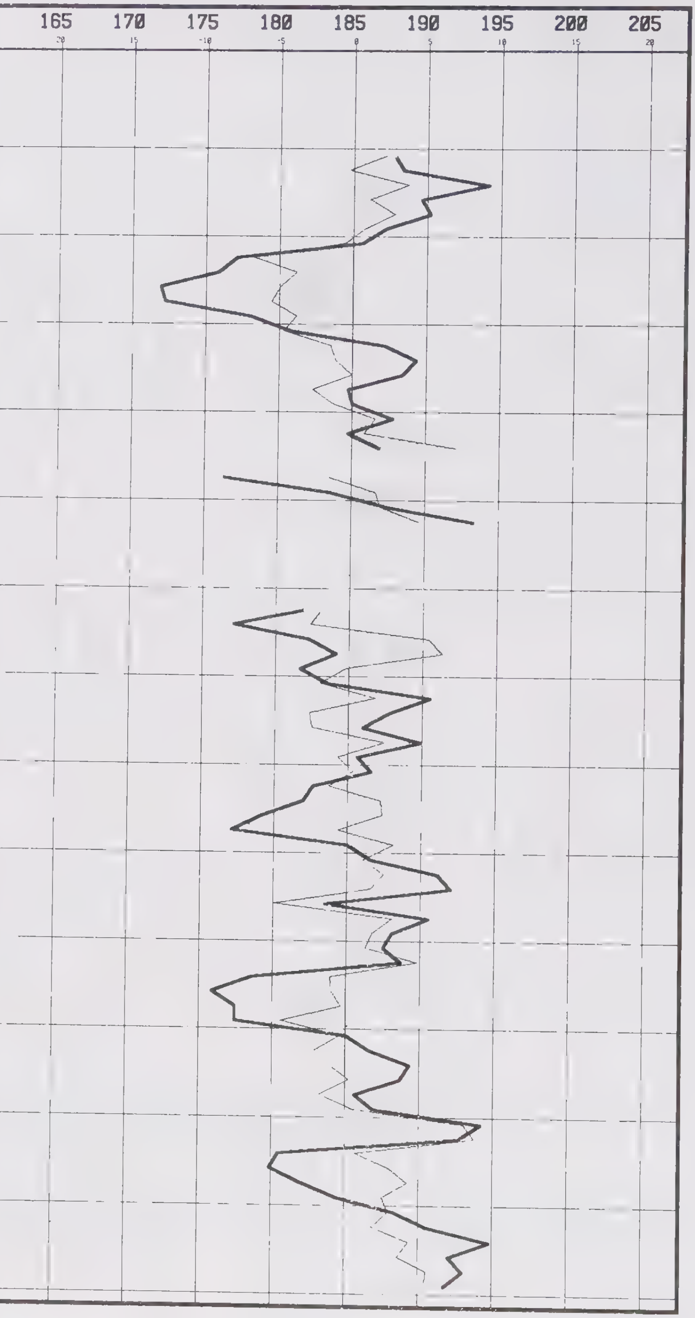
This appendix presents graphical plots of monthly means and monthly mean anomalies of various oceanic and atmospheric observations for the period 1960 to 1978 at Monterey, Calif. Anomalies were calculated as the difference between a monthly mean and the long term mean (1963-78) for the same month. Monthly means are shown as heavy lines and monthly anomalies as light lines. The data are presented in the following sequence:

1) sea level (cm),
2) adjusted sea level (cm),
3) surface atmospheric pressure (mb),
4) meridional wind stress (dynes/cm^2; positive northward),
5) zonal wind stress (dynes/cm^2; positive eastward),
6) offshore/onshore Ekman transport (t/s per 100 m of coastline; positive offshore),
7) Sverdrup transport (t/s per km; positive northward),
8) surface salinity (parts per thousand),
9) sea surface temperature (°C), and
10) dynamic height (cm).

NOAA-NMFS.PACIFIC ENVIRONMENTAL GROUP, MONTEREY, CALIFORNIA

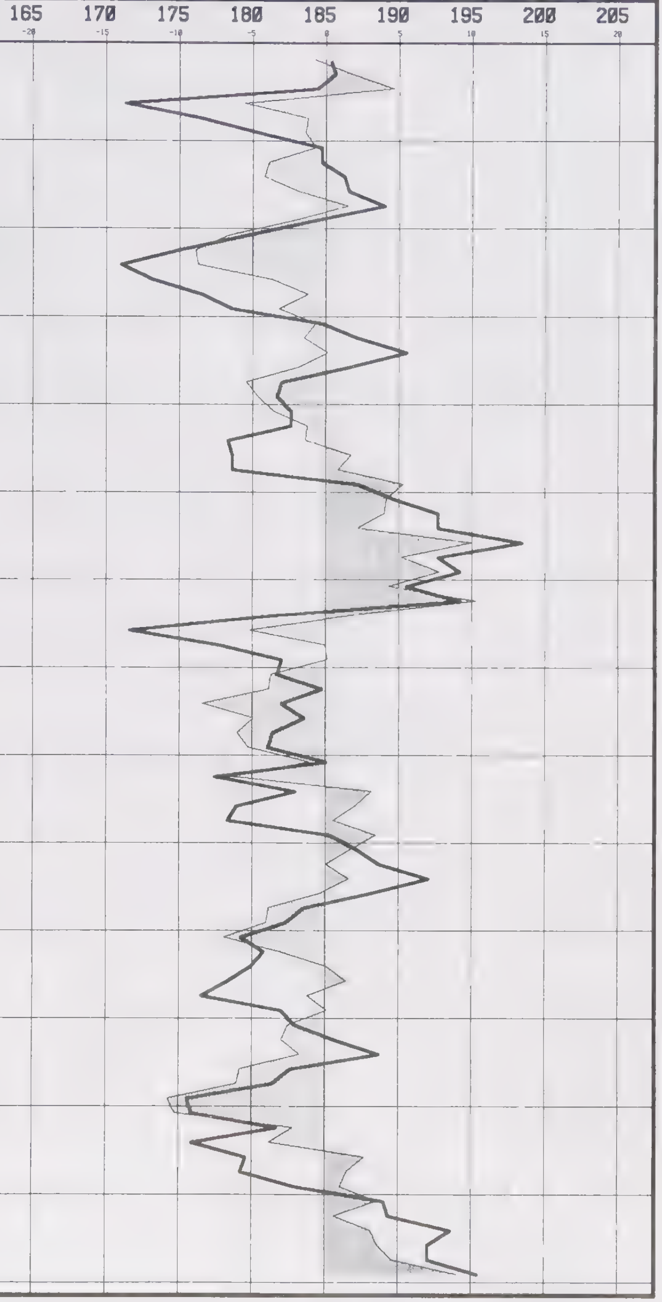
SEA LEVEL MONTEREY, CA BY MONTH

MONTH	VALUE	ANOMALY
196301	NO DATA	
2	NO DATA	
3	NO DATA	
4	NO DATA	
5	NO DATA	
6	NO DATA	
7	187.76	2.32
8	188.37	-.27
9	194.16	3.74
10	189.59	1.16
11	190.20	2.78
12	187.15	.81
196401	185.62	-.54
2	177.09	-6.79
3	175.87	-3.86
4	171.91	-4.94
5	172.21	-5.53
6	178.00	-3.84
7	180.75	-4.69
8	187.15	-1.49
9	189.28	-1.14
10	188.37	-.06
11	184.71	-2.70
12	185.01	-1.32
196501	187.76	1.59
2	184.71	.83
3	186.84	7.11
4	NO DATA	
5	176.17	-1.56
6	183.49	1.65
7	187.45	2.02
8	193.24	4.61
9	NO DATA	
10	NO DATA	
11	NO DATA	
12	NO DATA	
196601	NO DATA	
2	181.97	-1.91
3	177.09	-2.64
4	182.27	5.42
5	184.10	6.36
6	181.66	-.18
7	183.49	-1.94
8	190.50	1.87
9	187.76	-2.66
10	185.93	-2.50
11	189.89	2.48
12	185.62	-.71
196701	186.54	.37
2	182.58	-1.30
3	181.97	2.24
4	179.22	2.37
5	177.09	-.65
6	185.01	3.17
7	186.54	1.10
8	191.11	2.48
9	192.02	1.61
10	183.49	-4.94
11	190.50	3.09
12	188.06	1.73
196801	187.45	1.28
2	188.67	4.80
3	178.61	-1.12
4	175.87	-.98
5	177.39	-.35
6	177.39	-4.45
7	185.01	-.42
8	186.54	-2.10
9	189.28	-1.14
10	188.67	.24
11	185.62	-1.79
12	186.84	.51
196901	194.16	7.99
2	192.63	8.76
3	180.44	.71
4	179.83	2.98
5	181.97	4.23
6	184.40	2.56
7	188.37	2.93
8	190.50	1.87
9	194.77	4.35
10	192.02	3.60
11	192.94	5.53
12	191.72	5.38



SEA LEVEL MONTEREY, CA BY MONTH

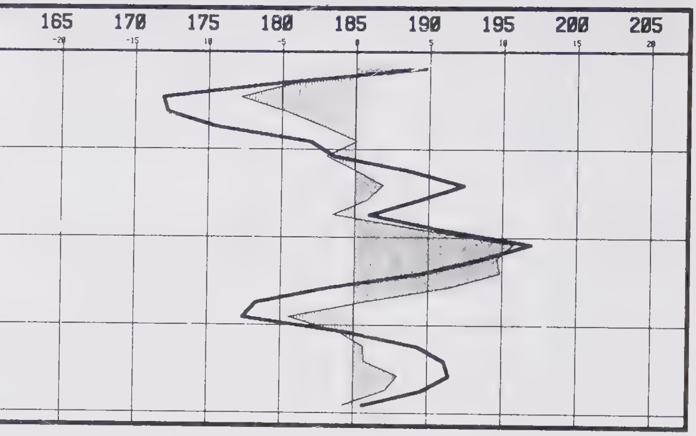
MONTH	VALUE	ANOMALY
197001	185.32	-.85
2	185.62	1.75
3	184.40	4.67
4	171.30	-5.55
5	176.48	-1.26
6	180.44	-1.40
7	184.71	-.72
8	184.71	-3.92
9	186.23	-4.19
10	186.54	-1.89
11	188.98	1.56
12	184.10	-2.24
197101	179.53	-6.64
2	174.96	-8.92
3	170.99	-8.74
4	173.13	-3.72
5	176.48	-1.26
6	178.61	-3.23
7	184.71	-.72
8	187.15	-1.49
9	190.50	.08
10	186.54	-1.89
11	181.97	-5.45
12	181.66	-4.67
197201	182.58	-3.59
2	182.58	-1.30
3	178.31	-1.42
4	178.61	1.76
5	178.61	.87
6	187.15	5.30
7	189.59	4.15
8	192.63	4.00
9	192.63	2.21
10	198.42	10.00
11	192.63	5.22
12	194.16	7.82
197301	190.50	4.33
2	194.16	10.28
3	181.36	1.63
4	171.60	-5.25
5	177.70	-.04
6	181.97	.12
7	181.66	-3.77
8	184.71	-3.92
9	181.97	-8.45
10	183.49	-4.94
11	181.36	-6.06
12	181.05	-5.28
197401	185.01	-1.15
2	177.39	-6.48
3	182.88	3.15
4	178.92	2.07
5	178.31	.57
6	185.32	3.47
7	187.15	1.71
8	188.67	.04
9	192.02	1.61
10	188.06	-.37
11	183.49	-3.92
12	182.27	-4.06
197501	179.22	-6.95
2	180.75	-3.13
3	179.83	.10
4	178.31	1.46
5	176.48	-1.26
6	181.97	.12
7	182.88	-2.55
8	185.62	-3.01
9	188.67	-1.75
10	182.58	-5.85
11	181.36	-6.06
12	175.56	-10.77
197601	175.87	-10.30
2	181.66	-2.21
3	175.87	-3.86
4	179.53	2.68
5	179.22	1.48
6	182.88	1.04
7	188.98	3.54
8	189.28	.65
9	193.55	3.13
10	192.02	3.60
11	192.02	4.61
12	195.38	9.04



NOAA-NMFS.PACIFIC ENVIRONMENTAL GROUP, MONTEREY, CALIFORNIA

SEA LEVEL MONTEREY, CA BY MONTH

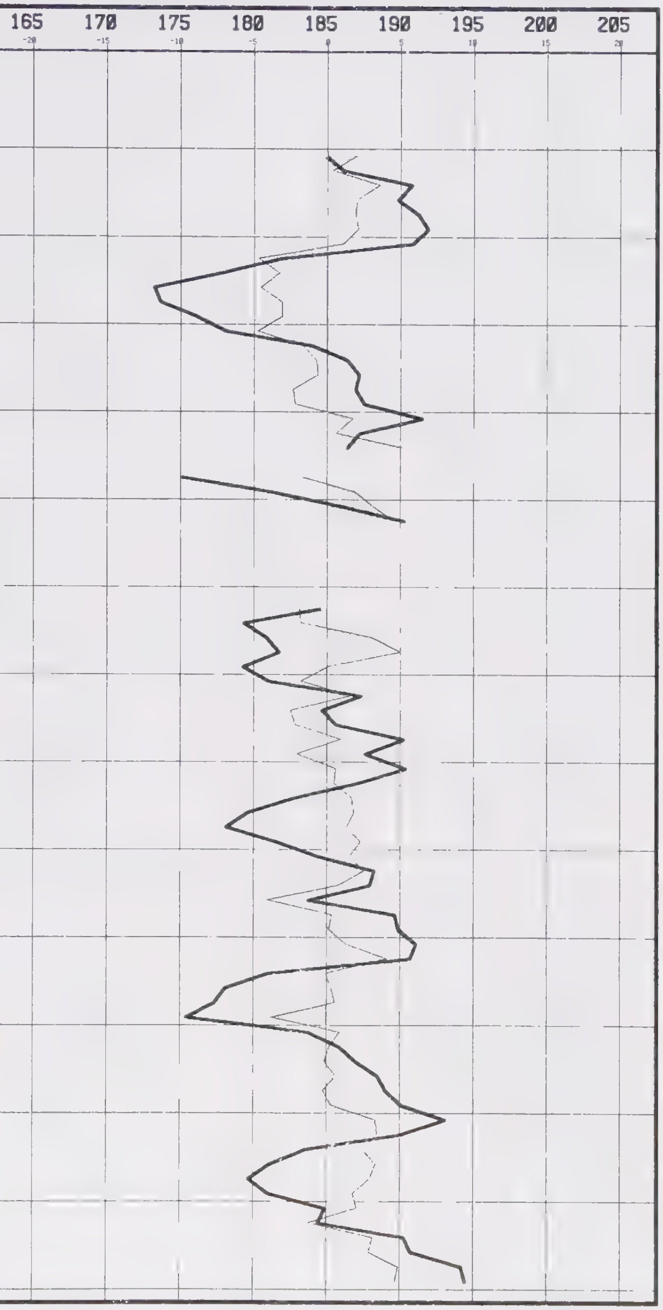
MONTH	VALUE	ANOMALY
197701	189.89	3.72
2	179.83	-4.04
3	171.91	-7.82
4	172.21	-4.64
5	175.56	-2.17
6	181.97	.12
7	183.49	-1.94
8	188.67	.04
9	192.33	1.91
10	189.28	.85
11	185.93	-1.48
12	190.80	4.47
197801	196.90	10.73
2	193.55	9.67
3	189.59	9.86
4	183.18	6.34
5	178.31	.57
6	177.39	-4.45
7	184.40	-1.03
8	189.28	.65
9	191.11	.69
10	191.41	2.99
11	189.59	2.17
12	185.62	-.71



NOAA-NMFS.PACIFIC ENVIRONMENTAL GROUP, MONTEREY, CALIFORNIA

ADJ. SEA LEVEL MONTEREY, CA BY MONTH

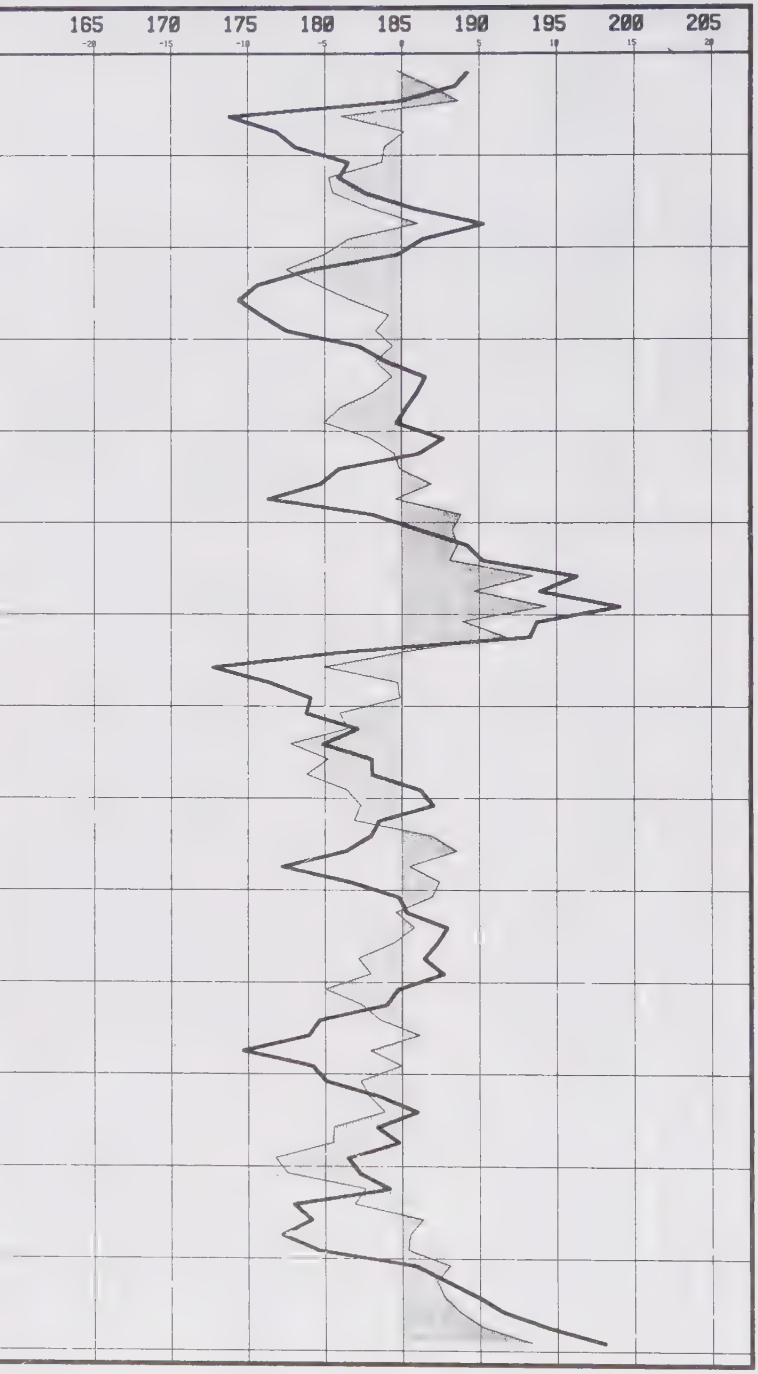
MONTH	VALUE	ANOMALY
196301	NO DATA	
2	NO DATA	
3	NO DATA	
4	NO DATA	
5	NO DATA	
6	NO DATA	
7	184.85	2.06
8	186.06	.42
9	190.75	3.62
10	189.78	1.98
11	191.19	1.95
12	191.84	2.12
196401	190.81	1.09
2	181.88	-4.69
3	177.76	-3.30
4	173.20	-4.56
5	173.60	-3.11
6	176.09	-3.10
7	178.04	-4.75
8	183.94	-1.70
9	186.37	-.76
10	187.16	-.64
11	186.90	-2.34
12	187.50	-2.22
196501	191.45	1.73
2	187.20	.63
3	186.33	5.27
4	NO DATA	
5	174.97	-1.74
6	181.08	1.89
7	185.94	3.15
8	190.23	4.59
9	NO DATA	
10	NO DATA	
11	NO DATA	
12	NO DATA	
196601	NO DATA	
2	184.66	-1.91
3	179.28	-1.78
4	180.86	3.10
5	181.69	4.98
6	179.25	.06
7	180.98	-1.81
8	187.29	1.65
9	184.65	-2.48
10	185.62	-2.18
11	190.18	.94
12	187.61	-2.11
196701	190.33	.61
2	187.07	.50
3	182.76	1.70
4	179.61	1.85
5	178.08	1.37
6	181.50	2.31
7	184.33	1.54
8	188.20	2.56
9	187.92	.79
10	183.68	-4.12
11	189.59	.35
12	189.85	.13
196801	191.04	1.32
2	190.66	4.09
3	181.00	-.06
4	178.06	.30
5	177.28	.57
6	175.38	-3.81
7	183.70	.91
8	185.83	.19
9	186.97	-.16
10	188.46	.66
11	189.01	-.23
12	190.03	.31
196901	193.05	3.33
2	190.02	3.45
3	183.53	2.47
4	181.12	3.36
5	179.66	2.95
6	181.00	1.81
7	184.86	2.07
8	184.39	-1.25
9	190.26	3.13
10	190.72	2.92
11	194.13	4.89
12	194.41	4.69



NOAA-NMFS.PACIFIC ENVIRONMENTAL GROUP. MONTEREY. CALIFORNIA

ADJ SEA LEVEL MONTEREY, CA BY MONTH

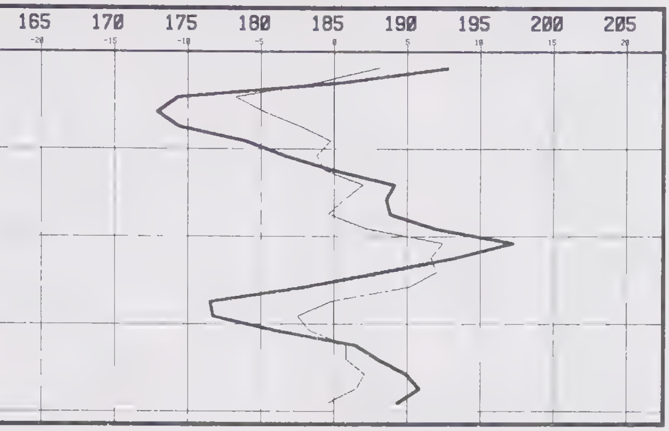
MONTH	VALUE	ANOMALY
197001	189.31	-.41
2	188.41	1.84
3	184.70	3.64
4	173.79	-3.97
5	176.87	.16
6	178.03	-1.16
7	181.50	-1.29
8	180.90	-4.74
9	182.62	-4.51
10	185.73	-2.07
11	190.27	1.03
12	186.29	-3.43
197101	184.72	-5.00
2	179.05	-7.52
3	175.58	-5.48
4	174.42	-3.34
5	175.87	-.84
6	177.50	-1.69
7	182.20	-.59
8	183.94	-1.70
9	186.49	-.64
10	185.93	-1.87
11	185.26	-3.98
12	184.65	-5.07
197201	187.67	-2.05
2	166.07	-.50
3	180.90	-.16
4	179.70	1.94
5	176.30	-.41
6	183.04	3.85
7	186.08	3.29
8	189.22	3.58
9	190.22	3.09
10	196.32	8.52
11	193.92	4.68
12	199.05	9.33
197301	193.69	3.97
2	193.25	6.68
3	181.15	.09
4	172.69	-5.07
5	176.39	-.32
6	179.06	-.13
7	178.75	-4.04
8	182.10	-3.54
9	179.86	-7.27
10	182.98	-4.82
11	183.05	-6.19
12	186.14	-3.58
197401	187.00	-2.72
2	183.48	-3.09
3	182.97	1.91
4	181.31	3.55
5	177.20	.49
6	181.61	2.42
7	184.74	1.95
8	185.26	-.38
9	187.92	.79
10	187.25	-.55
11	186.38	-2.86
12	187.66	-2.06
197501	184.71	-5.01
2	183.94	-2.63
3	179.62	-1.44
4	178.90	1.14
5	174.67	-2.04
6	179.16	-.03
7	180.07	-2.72
8	183.51	-2.13
9	185.96	-1.17
10	183.37	-4.43
11	184.74	-4.50
12	181.46	-8.26
197601	182.26	-7.46
2	184.15	-2.42
3	177.96	-3.10
4	179.12	1.36
5	177.21	.50
6	179.57	.36
7	185.87	3.08
8	187.87	2.23
9	189.84	2.71
10	191.52	3.72
11	194.42	5.18
12	198.07	8.35



NOAA-NMFS.PACIFIC ENVIRONMENTAL GROUP, MONTEREY, CALIFORNIA

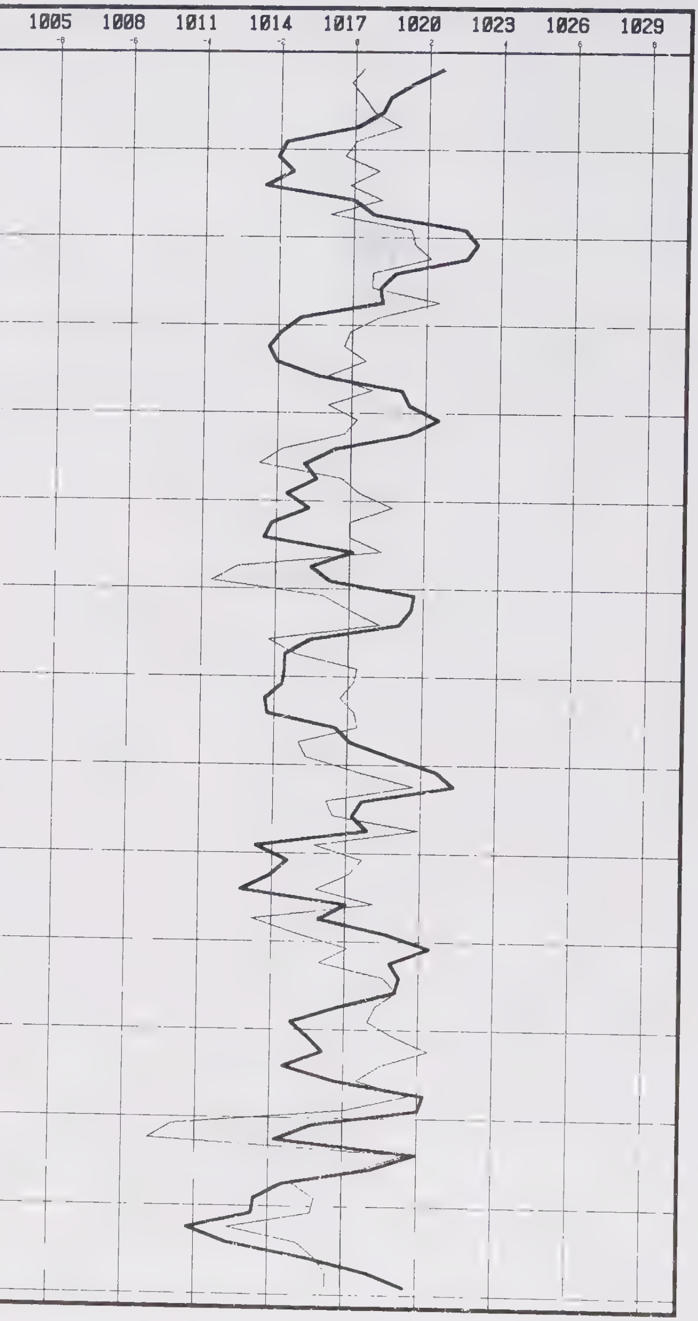
ADJ. SEA LEVEL MONTEREY, CA BY MONTH

MONTH	VALUE	ANOMALY
197701	192.88	3.16
2	185.52	-1.05
3	174.30	-6.76
4	172.90	-4.86
5	174.36	-2.35
6	178.96	-.23
7	181.58	-1.21
8	184.96	-.68
9	189.12	1.99
10	188.57	.77
11	188.82	-.42
12	191.90	2.18
197801	197.19	7.47
2	193.24	6.67
3	188.08	7.02
4	182.98	5.22
5	176.50	-.21
6	176.68	-2.51
7	181.10	-1.69
8	186.47	.83
9	188.00	.87
10	189.91	2.11
11	190.78	1.54
12	189.31	-.41



PRESSURE BY MONTH

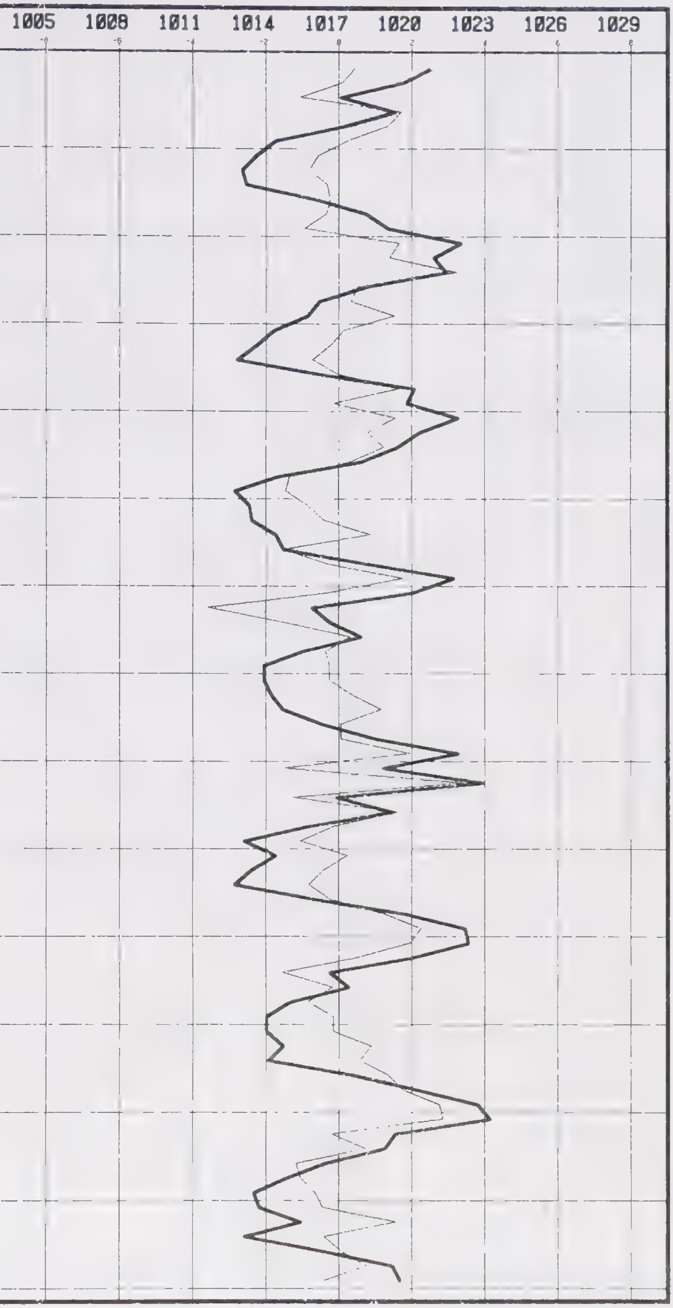
MONTH	VALUE	ANOMALY
196301	1020.60	.27
2	1019.40	-.10
3	1018.40	.24
4	1018.10	.52
5	1017.10	1.24
6	1014.20	.04
7	1013.90	-.26
8	1014.50	.69
9	1013.40	-.12
10	1017.00	.76
11	1017.80	-.64
12	1021.50	1.56
196401	1022.00	1.67
2	1021.60	2.10
3	1018.70	.54
4	1018.10	.52
5	1018.20	2.34
6	1014.90	.74
7	1014.10	-.06
8	1013.60	-.21
9	1013.90	.38
10	1015.60	-.64
11	1019.00	.56
12	1019.30	-.64
196501	1020.50	.17
2	1019.30	-.20
3	1016.30	-1.86
4	1015.10	-2.48
5	1015.60	-.26
6	1014.40	.24
7	1015.30	1.14
8	1013.80	-.01
9	1013.50	-.02
10	1017.10	.86
11	1015.40	-3.04
12	1016.20	-3.74
196601	1019.60	-.73
2	1019.50	.00
3	1019.00	.84
4	1015.40	-2.18
5	1014.40	-1.46
6	1014.40	.24
7	1014.30	.14
8	1013.60	-.21
9	1013.70	.18
10	1016.50	.26
11	1017.10	-1.34
12	1018.80	-1.14
196701	1020.60	.27
2	1021.30	1.80
3	1017.60	-.56
4	1017.20	-.38
5	1017.80	1.94
6	1013.30	-.86
7	1014.60	.44
8	1013.90	.09
9	1012.70	-.82
10	1017.00	.76
11	1015.90	-2.54
12	1018.60	-1.34
196801	1020.40	.07
2	1018.80	-.70
3	1019.20	1.04
4	1019.00	1.42
5	1016.70	.84
6	1014.80	.64
7	1015.50	1.34
8	1016.10	2.29
9	1014.50	.98
10	1016.60	.36
11	1020.20	1.76
12	1020.00	.06
196901	1015.70	-4.63
2	1014.20	-5.30
3	1019.90	1.74
4	1018.10	.52
5	1014.50	-1.36
6	1013.40	-.76
7	1013.30	-.86
8	1010.70	-3.11
9	1012.30	-1.22
10	1015.50	-.74
11	1018.00	-.44
12	1019.50	-.44



NOAA-NMFS, PACIFIC ENVIRONMENTAL GROUP, MONTEREY, CALIFORNIA

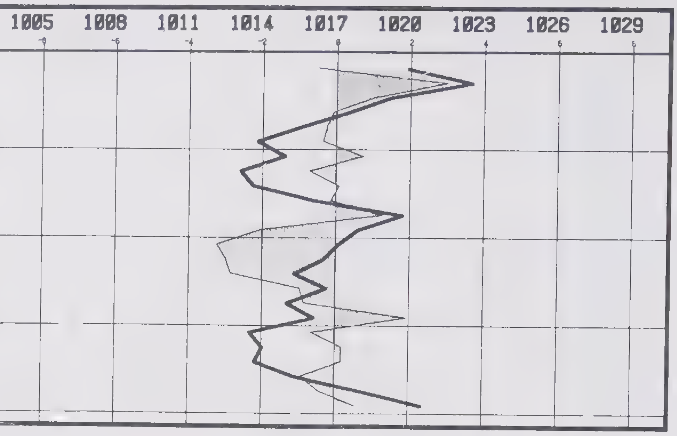
PRESSURE BY MONTH

MONTH	VALUE	ANOMALY
197001	1020.80	.47
2	1019.60	.10
3	1017.10	-1.06
4	1019.30	1.72
5	1017.20	1.34
6	1014.40	.24
7	1013.60	-.56
8	1013.00	-.81
9	1013.20	-.32
10	1016.00	-.24
11	1018.10	-.34
12	1019.00	-.94
197101	1022.00	1.67
2	1020.90	1.40
3	1021.40	3.24
4	1013.10	.52
5	1016.20	.34
6	1015.70	1.54
7	1014.30	.14
8	1013.60	-.21
9	1012.80	-.72
10	1016.20	-.04
11	1020.10	1.66
12	1019.80	-.14
197201	1021.90	1.57
2	1020.30	.80
3	1019.40	1.24
4	1017.90	.32
5	1014.50	-1.36
6	1012.70	-1.46
7	1013.30	-.86
8	1013.40	-.41
9	1014.40	.88
10	1014.70	-1.54
11	1018.10	-.34
12	1021.70	1.76
197301	1020.00	-.33
2	1015.90	-3.60
3	1016.60	-1.56
4	1017.90	.32
5	1015.50	-.36
6	1013.90	-.26
7	1013.90	-.26
8	1014.20	.39
9	1014.70	1.18
10	1016.30	.06
11	1018.50	.06
12	1021.90	1.96
197401	1018.80	-1.53
2	1022.90	3.40
3	1016.90	-1.26
4	1019.20	1.62
5	1015.70	-.16
6	1013.10	-1.06
7	1014.40	.24
8	1013.40	-.41
9	1012.70	-.82
10	1016.00	-.24
11	1019.70	1.26
12	1022.20	2.26
197501	1022.30	1.97
2	1020.00	.50
3	1016.60	-1.56
4	1017.40	-.18
5	1015.00	-.86
6	1014.00	-.16
7	1014.00	-.16
8	1014.70	.89
9	1014.10	.58
10	1017.60	1.36
11	1020.20	1.76
12	1022.70	2.75
197601	1023.20	2.87
2	1019.30	-.20
3	1018.90	.74
4	1016.40	-1.18
5	1014.80	-1.06
6	1013.50	-.66
7	1013.70	-.46
8	1015.40	1.59
9	1013.10	-.42
10	1016.30	.06
11	1019.20	.76
12	1019.50	-.44



PRESSURE BY MONTH

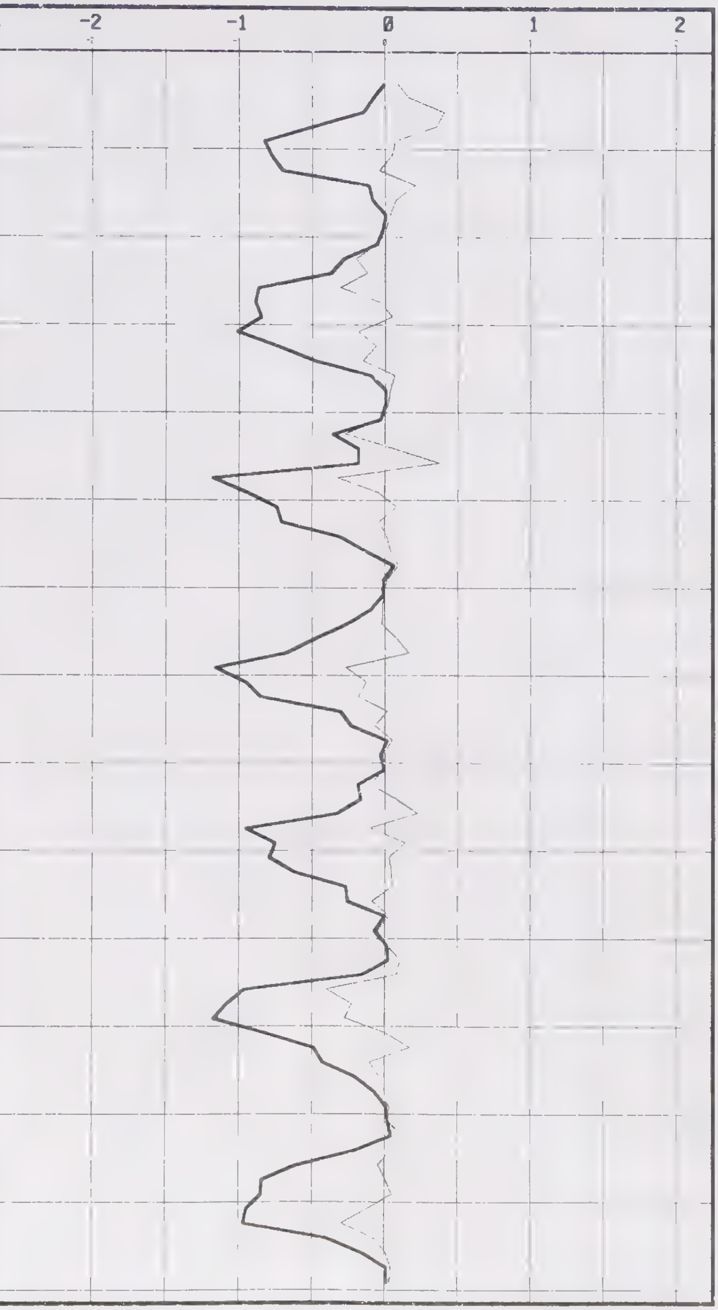
MONTH	VALUE	ANOMALY
197701	1019.80	-.53
2	1022.50	3.00
3	1019.20	1.04
4	1017.50	-.08
5	1015.60	-.26
6	1013.80	-.36
7	1014.90	.74
8	1013.10	-.71
9	1013.60	.08
10	1016.10	-.14
11	1019.70	1.26
12	1017.90	-2.04
197801	1017.10	-3.23
2	1016.50	-3.00
3	1015.30	-2.86
4	1016.60	-.98
5	1015.00	-.86
6	1016.10	1.94
7	1013.50	-.66
8	1014.00	.19
9	1013.70	.18
10	1015.30	-.94
11	1018.00	-.44
12	1020.50	.56



NOAA-NMFS.PACIFIC ENVIRONMENTAL GROUP, MONTEREY, CALIFORNIA

N. COMP. WIND STRESS BY MONTH

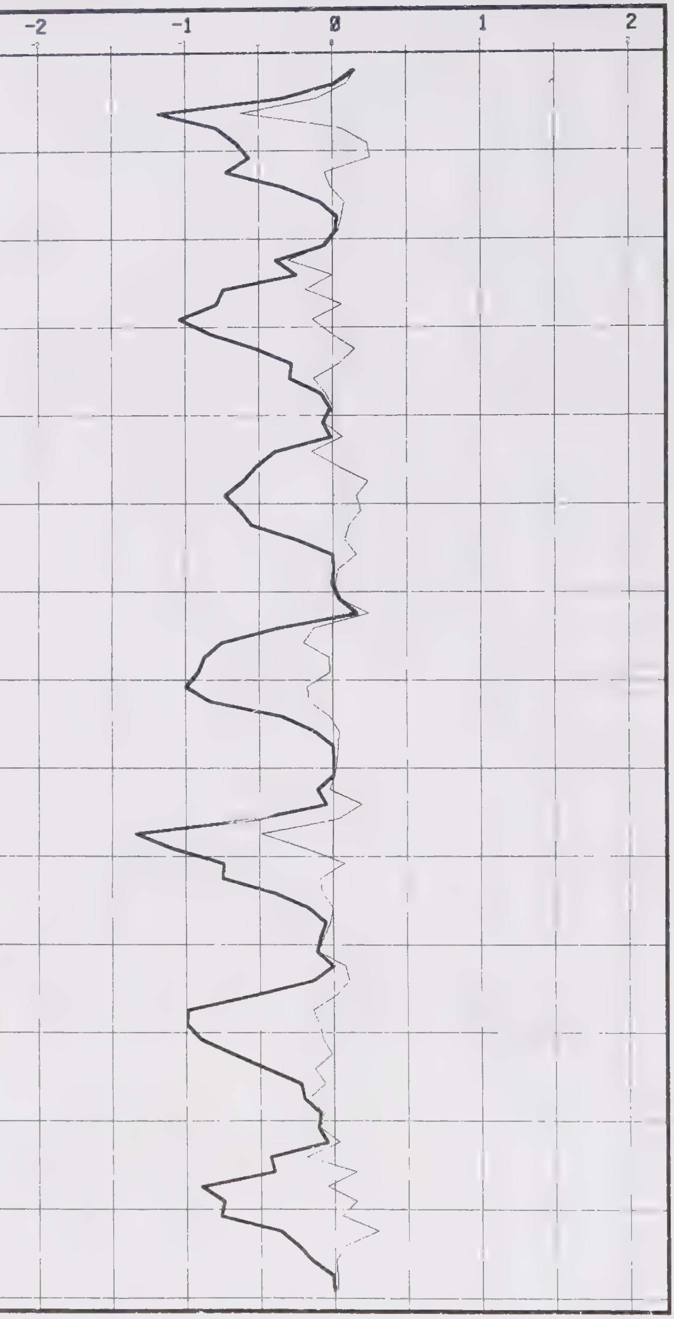
MONTH	VALUE	ANOMALY
196301	-.05	-.05
2	0.00	.08
3	-.08	.17
4	-.15	.41
5	-.50	.36
6	-.83	.07
7	-.78	.05
8	-.71	-.04
9	-.11	.21
10	-.09	.08
11	0.00	.04
12	-.02	.01
196401	-.06	-.05
2	-.29	-.20
3	-.37	-.13
4	-.87	-.31
5	-.89	-.04
6	-.85	.05
7	-1.01	-.19
8	-.73	-.07
9	-.48	-.16
10	-.10	.07
11	0.00	.04
12	-.00	.02
196501	-.04	-.03
2	-.36	-.28
3	-.19	.06
4	-.18	.38
5	-1.18	-.33
6	-.95	-.05
7	-.74	.09
8	-.71	-.04
9	-.31	.02
10	-.13	.04
11	.06	.10
12	-.01	.02
196601	-.02	-.01
2	-.10	-.02
3	-.27	-.02
4	-.48	.08
5	-.69	.17
6	-1.17	-.27
7	-.96	-.13
8	-.85	-.19
9	-.31	.01
10	-.24	-.07
11	.01	.05
12	-.04	-.01
196701	-.01	-.01
2	-.19	-.11
3	-.17	.08
4	-.34	.22
5	-.95	-.10
6	-.76	.14
7	-.80	.03
8	-.62	.04
9	-.27	.05
10	-.26	-.09
11	-.01	.03
12	-.08	-.05
196801	.01	.02
2	.02	.11
3	-.16	.09
4	-.96	-.40
5	-1.08	-.23
6	-1.17	-.28
7	-.82	.00
8	-.49	.18
9	-.43	-.11
10	-.21	-.04
11	-.08	-.04
12	.01	.03
196901	.02	.02
2	.04	.13
3	-.21	.04
4	-.61	-.05
5	-.84	.01
6	-.85	.05
7	-.95	-.12
8	-.97	-.30
9	-.40	-.08
10	-.16	.01
11	.01	.05
12	.01	.03



NOAA-NMFS.PACIFIC ENVIRONMENTAL GROUP. MONTEREY. CALIFORNIA

N. COMP. WIND STRESS BY MONTH

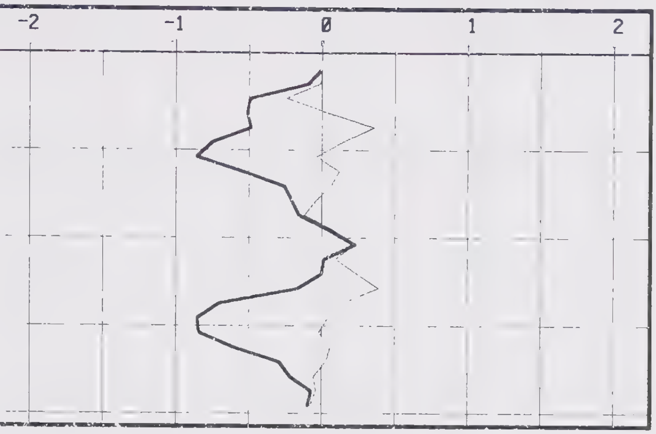
MONTH	VALUE	ANOMALY
197001	.16	.16
2	.01	.10
3	-.36	-.11
4	-1.19	-.63
5	-.79	.06
6	-.66	.24
7	-.57	.26
8	-.72	-.06
9	-.34	-.02
10	-.09	.08
11	.02	.06
12	.01	.04
197101	-.06	-.06
2	-.39	-.31
3	-.25	-.00
4	-.74	-.18
5	-.79	.06
6	-1.04	-.14
7	-.83	-.00
8	-.52	.15
9	-.28	.05
10	-.30	-.13
11	-.09	-.05
12	-.02	.00
197201	-.07	-.06
2	-.02	.07
3	-.39	-.15
4	-.52	.04
5	-.61	.24
6	-.74	.16
7	-.64	.19
8	-.56	.11
9	-.24	.08
10	-.01	.16
11	.00	.04
12	-.01	.02
197301	.04	.04
2	.16	.25
3	-.38	-.13
4	-.76	-.20
5	-.88	-.02
6	-.92	-.02
7	-1.00	-.18
8	-.83	-.17
9	-.35	-.02
10	-.13	.04
11	-.00	.03
12	.00	.03
197401	.00	.01
2	-.11	-.02
3	-.05	.20
4	-.53	.03
5	-1.34	-.49
6	-1.09	-.19
7	-.75	.08
8	-.75	-.08
9	-.40	-.07
10	-.17	-.00
11	-.06	-.02
12	-.09	-.07
197501	-.12	-.11
2	-.00	.08
3	-.14	.11
4	-.54	.02
5	-.99	-.14
6	-1.00	-.10
7	-.90	-.07
8	-.68	-.01
9	-.46	-.13
10	-.23	-.06
11	-.21	-.17
12	-.10	-.07
197601	-.11	-.10
2	-.05	.03
3	-.44	-.19
4	-.41	.15
5	-.90	-.05
6	-.75	.15
7	-.77	.05
8	-.37	.30
9	-.25	.07
10	-.16	.01
11	-.02	.02
12	-.01	.02



NOAA-NMFS,PACIFIC ENVIRONMENTAL GROUP, MONTEREY, CALIFORNIA

N. COMP. WIND STRESS BY MONTH

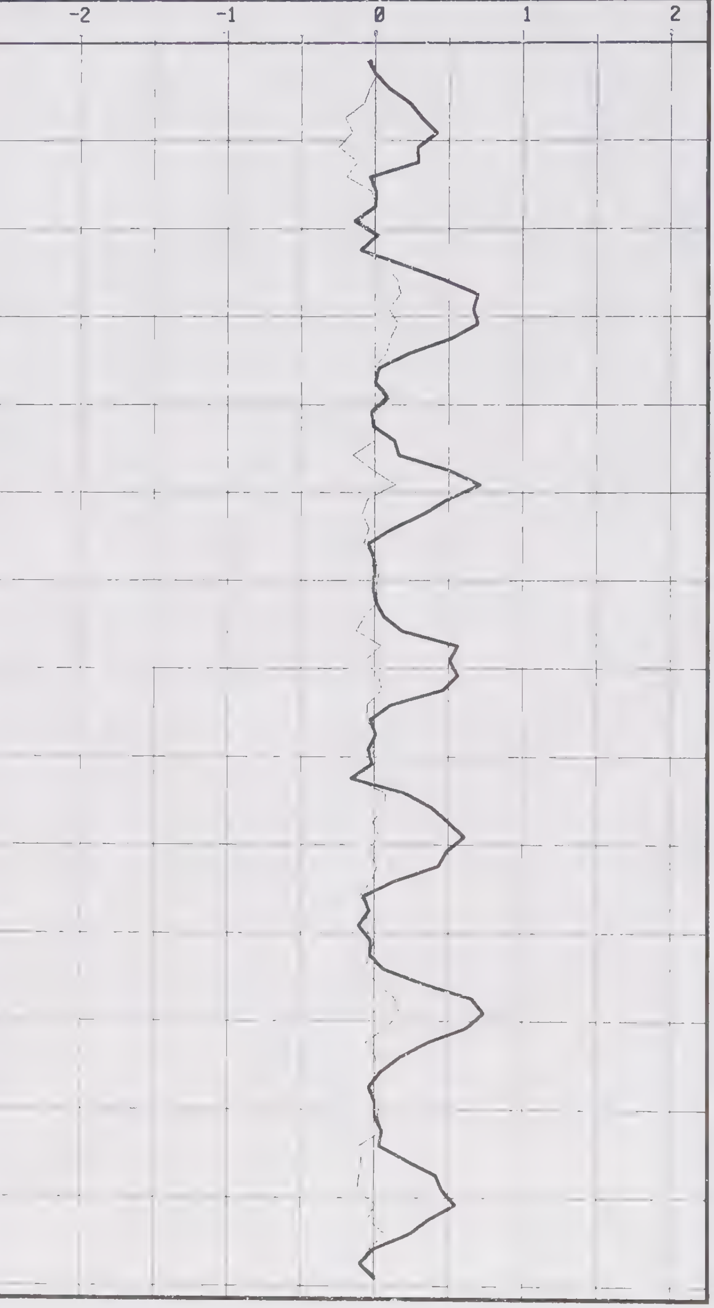
MONTH	VALUE	ANOMALY
197701	-.01	.00
2	-.10	-.01
3	-.49	-.25
4	-.52	.05
5	-.49	.36
6	-.76	.14
7	-.86	-.03
8	-.55	.12
9	-.26	.06
10	-.21	-.04
11	-.16	-.12
12	.05	.07
197801	.22	.23
2	.01	.09
3	-.01	.24
4	-.17	.39
5	-.70	.15
6	-.85	.04
7	-.85	-.02
8	-.61	.06
9	-.30	.03
10	-.22	-.05
11	-.08	-.04
12	-.10	-.08



NOAA-NMFS, PACIFIC ENVIRONMENTAL GROUP, MONTEREY, CALIFORNIA

EAST COMP. WIND STRESS BY MONTH

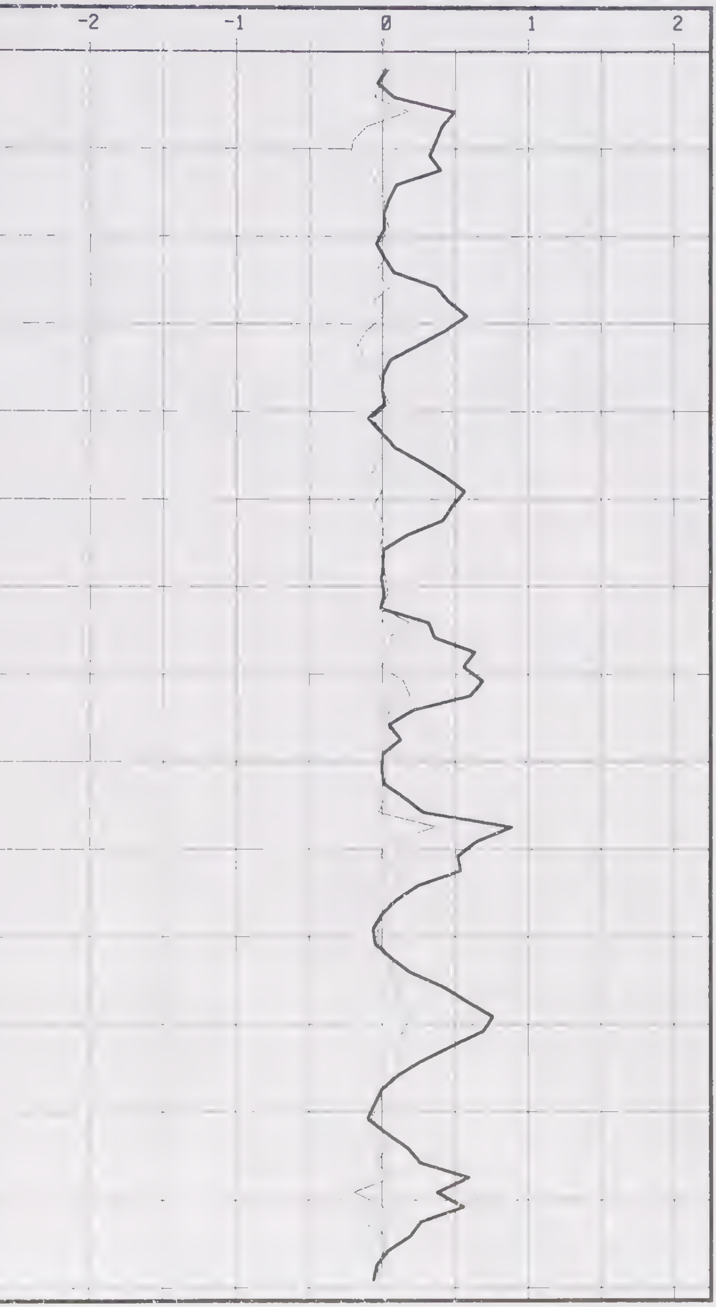
MONTH	VALUE	ANOMALY
196301	-.06	-.03
2	.00	.01
3	.09	-.04
4	.23	-.07
5	.31	-.20
6	.41	-.16
7	.29	-.25
8	.29	-.12
9	-.04	-.19
10	.00	-.02
11	0.00	.01
12	-.14	-.11
196401	.01	.04
2	-.10	-.09
3	.19	.06
4	.46	.15
5	.69	.18
6	.66	.09
7	.70	.16
8	.52	.10
9	.24	.08
10	.03	-.00
11	0.00	.01
12	.08	.11
196501	-.03	-.00
2	-.01	-.00
3	.13	-.00
4	.16	-.15
5	.50	-.02
6	.71	.14
7	.49	-.05
8	.33	-.09
9	.12	-.04
10	-.05	-.07
11	-.01	.00
12	-.00	.03
196601	-.02	.01
2	.01	.02
3	.06	-.07
4	.18	-.12
5	.56	.04
6	.51	-.06
7	.56	.02
8	.46	.05
9	.11	-.05
10	-.03	-.05
11	.01	.02
12	-.05	-.01
196701	-.02	.01
2	-.16	-.15
3	.21	.07
4	.38	.08
5	.50	-.01
6	.61	.04
7	.49	-.05
8	.43	.02
9	.14	-.02
10	-.07	-.10
11	-.04	-.03
12	-.11	-.07
196801	-.03	-.00
2	-.03	-.02
3	.06	-.07
4	.33	.02
5	.65	.14
6	.74	.17
7	.62	.08
8	.35	-.06
9	.17	.01
10	.04	.01
11	-.04	-.03
12	.00	.04
196901	.00	.03
2	.05	.06
3	.03	-.10
4	.22	-.09
5	.41	-.10
6	.45	-.11
7	.55	.01
8	.37	-.04
9	.24	.08
10	-.00	-.03
11	-.10	-.09
12	-.00	.03



NOAA-NMFS, PACIFIC ENVIRONMENTAL GROUP, MONTEREY, CALIFORNIA

EAST COMP. WIND STRESS BY MONTH

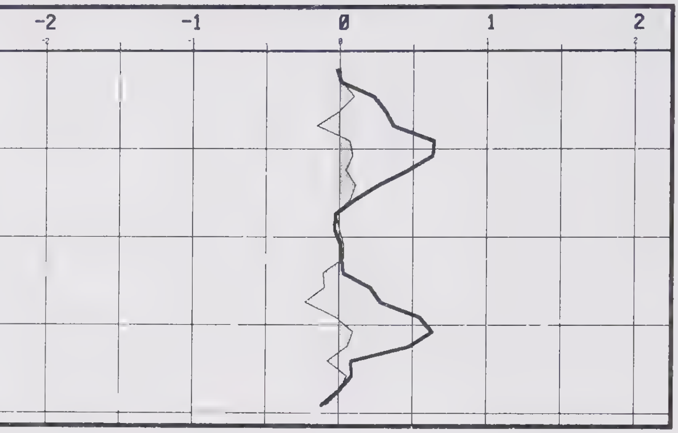
MONTH	VALUE	ANOMALY
197001	.03	.06
2	-.03	-.02
3	.08	-.05
4	.49	.18
5	.41	-.11
6	.36	-.20
7	.32	-.22
8	.40	-.02
9	.09	-.07
10	.04	.01
11	.01	.01
12	.01	.05
197101	-.04	-.02
2	.01	.02
3	.03	-.05
4	.36	.06
5	.45	-.07
6	.57	.00
7	.43	-.11
8	.24	-.17
9	.05	-.11
10	0.00	-.03
11	-.01	.00
12	.01	.04
197201	-.10	-.07
2	-.01	.00
3	.09	-.05
4	.27	-.04
5	.43	-.08
6	.56	-.01
7	.47	-.06
8	.41	-.00
9	.17	.01
10	.00	-.02
11	-.00	.01
12	-.01	.02
197301	.01	.04
2	-.01	-.00
3	.32	.19
4	.36	.05
5	.63	.11
6	.56	-.01
7	.68	.15
8	.60	.19
9	.21	.05
10	.04	.02
11	.13	.13
12	.00	.03
197401	-.00	.02
2	.01	.02
3	.15	.02
4	.28	-.03
5	.89	.37
6	.64	.07
7	.52	-.02
8	.54	.12
9	.25	.09
10	.10	.07
11	-.01	.00
12	-.06	-.03
197501	-.05	-.02
2	.06	.07
3	.20	.06
4	.43	.12
5	.59	.07
6	.75	.19
7	.69	.15
8	.47	.06
9	.28	.12
10	.11	.08
11	-.00	.00
12	-.05	-.02
197601	-.10	-.08
2	.03	.04
3	.17	.04
4	.26	-.05
5	.59	.07
6	.37	-.19
7	.56	.02
8	.27	-.15
9	.19	.03
10	.04	.01
11	-.04	-.03
12	-.06	-.02



NOAA-NMFS.PACIFIC ENVIRONMENTAL GROUP, MONTEREY, CALIFORNIA

EAST COMP. WIND STRESS BY MONTH

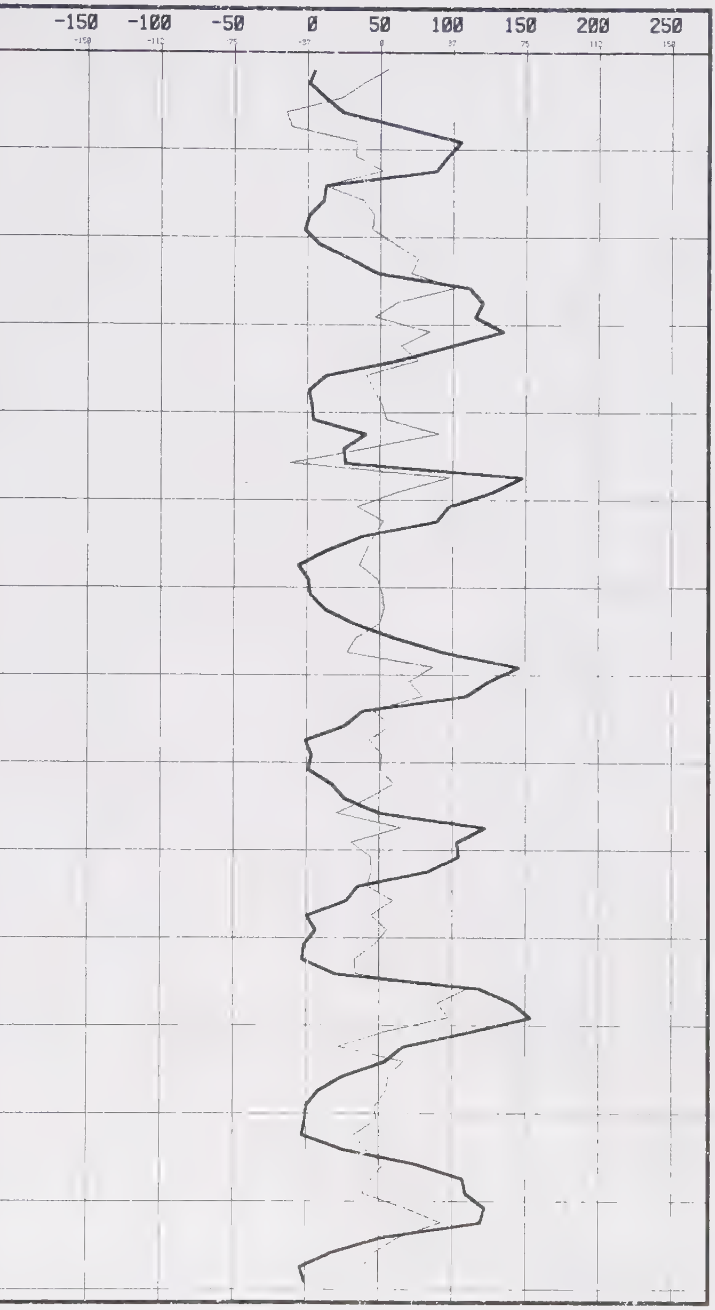
MONTH	VALUE	ANOMALY
197701	-.02	.00
2	.00	.01
3	.23	.10
4	.31	.00
5	.36	-.15
6	.64	.07
7	.63	.09
8	.46	.05
9	.27	.11
10	.10	.07
11	-.03	-.02
12	-.03	.00
197801	.00	.03
2	.02	.03
3	.02	-.11
4	.21	-.10
5	.28	-.24
6	.55	-.02
7	.63	.09
8	.47	.06
9	.08	-.08
10	.08	.06
11	0.00	.01
12	-.12	-.08



EKMAN TSPT

BY MONTH

MONTH	VALUE	ANOMALY
196301	5.00	4.56
2	1.00	-8.63
3	12.00	-19.94
4	24.00	-48.25
5	65.00	-45.81
6	105.00	-12.44
7	96.00	-12.63
8	88.00	1.00
9	12.00	-29.31
10	11.00	-9.00
11	1.00	-3.31
12	-2.00	-4.00
196401	8.00	7.56
2	29.00	19.38
3	48.00	16.06
4	111.00	38.75
5	120.00	9.19
6	115.00	-2.44
7	134.00	25.38
8	98.00	11.00
9	61.00	19.69
10	13.00	-7.00
11	1.00	-3.31
12	3.00	1.00
196501	4.00	3.56
2	40.00	30.38
3	25.00	-6.94
4	26.00	-46.25
5	147.00	36.19
6	127.00	9.56
7	97.00	-11.63
8	89.00	2.00
9	38.00	-3.31
10	13.00	-7.00
11	-6.00	-10.31
12	1.00	-1.00
196601	2.00	1.56
2	12.00	2.38
3	32.00	.06
4	60.00	-12.25
5	94.00	-16.81
6	145.00	27.56
7	124.00	15.38
8	109.00	22.00
9	38.00	-3.31
10	26.00	6.00
11	-1.00	-5.31
12	3.00	1.00
196701	1.00	.56
2	17.00	7.38
3	26.00	-5.94
4	50.00	-22.25
5	122.00	11.19
6	103.00	-14.44
7	104.00	-4.63
8	83.00	-4.00
9	35.00	-6.31
10	27.00	7.00
11	0.00	-4.31
12	6.00	4.00
196801	-2.00	-2.44
2	-3.00	-12.63
3	20.00	-11.94
4	118.00	45.75
5	141.00	30.19
6	153.00	35.56
7	111.00	2.38
8	66.00	-21.00
9	54.00	12.69
10	25.00	5.00
11	8.00	3.69
12	0.00	-2.00
196901	-1.00	-1.44
2	-3.00	-12.63
3	25.00	-6.94
4	75.00	2.75
5	107.00	-3.81
6	109.00	-8.44
7	122.00	13.38
8	119.00	32.00
9	52.00	10.69
10	18.00	-2.00
11	-4.00	-8.31
12	-1.00	-3.00

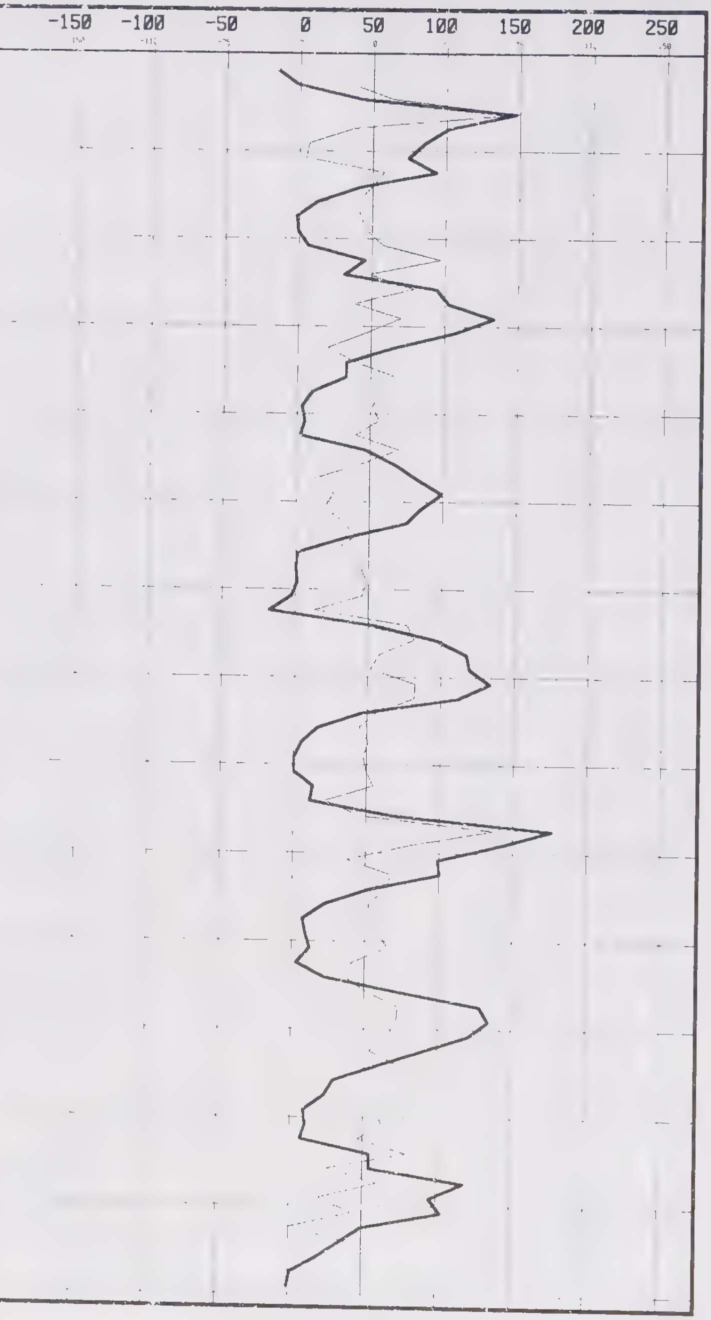


NOAA-NMFS, PACIFIC ENVIRONMENTAL GROUP, MONTEREY, CALIFORNIA

EKMAN TSPT

BY MONTH

MONTH	VALUE	ANOMALY
197001	-16.00	-16.44
2	-2.00	-11.63
3	42.00	10.06
4	147.00	74.75
5	101.00	-9.81
6	85.00	-32.44
7	74.00	-34.63
8	93.00	6.00
9	41.00	-.31
10	12.00	-8.00
11	-2.00	-6.31
12	-1.00	-3.00
197101	6.00	5.56
2	45.00	35.38
3	31.00	-.94
4	94.00	21.75
5	102.00	-8.81
6	133.00	15.56
7	106.00	-2.63
8	65.00	-22.00
9	33.00	-8.31
10	33.00	13.00
11	10.00	5.69
12	3.00	1.00
197201	5.00	4.56
2	2.00	-7.63
3	47.00	15.06
4	67.00	-5.25
5	82.00	-28.81
6	99.00	-18.44
7	85.00	-23.63
8	75.00	-12.00
9	33.00	-8.31
10	1.00	-19.00
11	0.00	-4.31
12	1.00	-1.00
197301	-3.00	-3.44
2	-18.00	-27.63
3	52.00	20.06
4	96.00	23.75
5	117.00	6.19
6	119.00	1.56
7	133.00	24.38
8	111.00	24.00
9	46.00	4.69
10	16.00	-4.00
11	5.00	.69
12	0.00	-2.00
197401	0.00	-.44
2	13.00	3.38
3	11.00	-20.94
4	68.00	-4.25
5	176.00	65.19
6	141.00	23.56
7	93.00	-9.63
8	100.00	13.00
9	52.00	10.69
10	22.00	2.00
11	7.00	2.69
12	9.00	7.00
197501	12.00	11.56
2	3.00	-6.63
3	22.00	-9.94
4	73.00	.75
5	128.00	17.19
6	134.00	16.56
7	121.00	12.33
8	90.00	3.00
9	59.00	17.69
10	29.00	9.00
11	23.00	18.69
12	9.00	7.00
197601	10.00	9.56
2	7.00	-2.63
3	54.00	27.06
4	54.00	-18.25
5	118.00	7.19
6	95.00	-22.44
7	103.00	-5.63
8	49.00	-38.00
9	34.00	-7.31
10	19.00	-1.00
11	1.00	-3.31
12	-1.00	-3.00

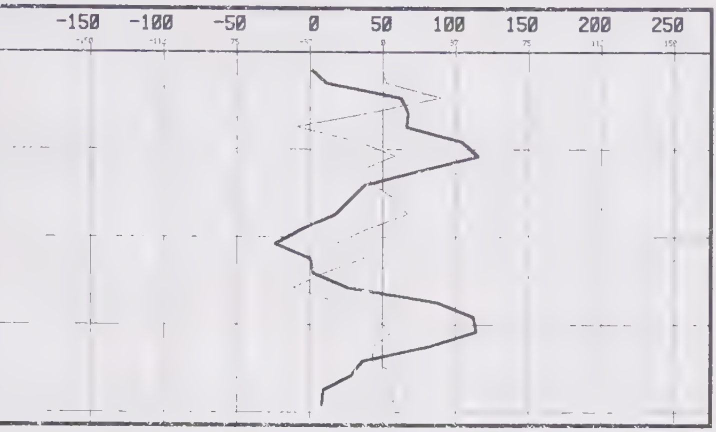


NOAA-NMFS. PACIFIC ENVIRONMENTAL GROUP, MONTEREY, CALIFORNIA

EKMAN TSPT

BY MONTH

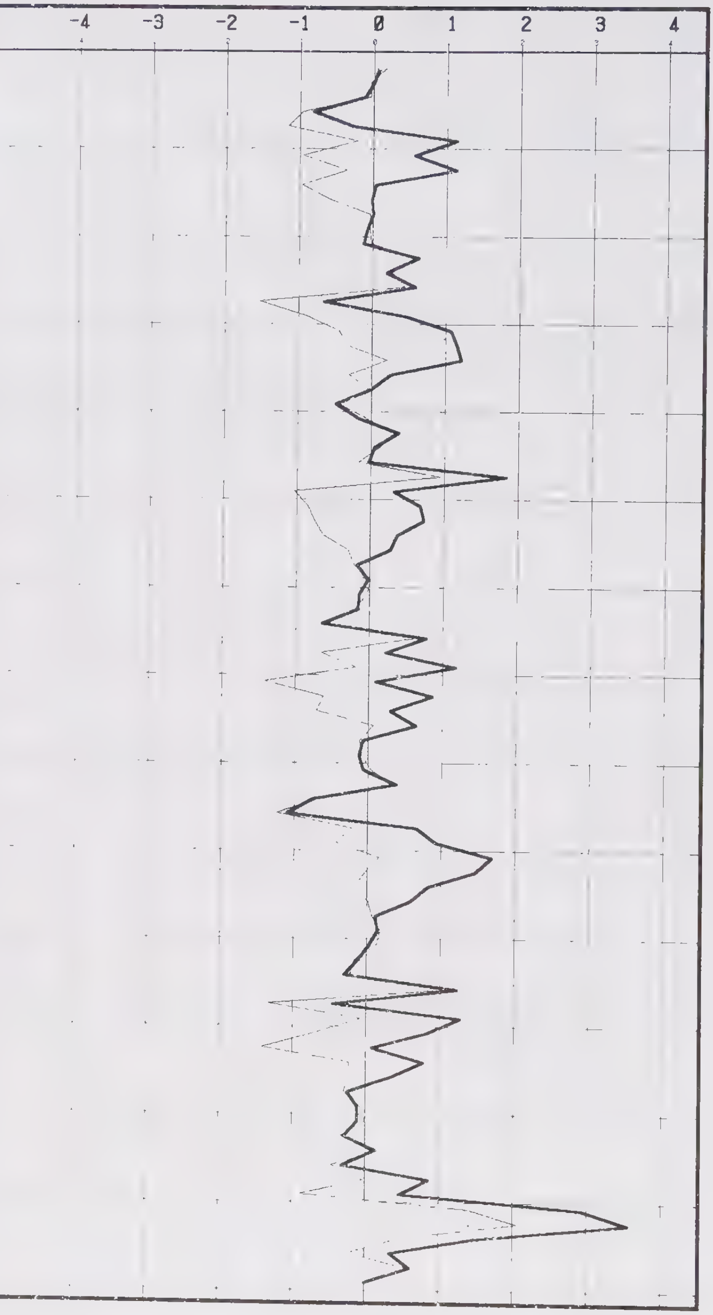
MONTH	VALUE	ANOMALY
197701	0.00	-.44
2	11.00	1.38
3	62.00	30.06
4	67.00	-5.25
5	66.00	-44.61
6	104.00	-13.44
7	115.00	6.38
8	75.00	-12.00
9	37.00	-4.31
10	27.00	7.00
11	17.00	12.69
12	-6.00	-8.00
197801	-24.00	-21.44
2	0.00	-9.63
3	2.00	-29.94
4	26.00	-46.25
5	87.00	-23.81
6	112.00	-5.44
7	114.00	5.38
8	82.00	-5.00
9	36.00	-5.31
10	28.00	8.00
11	9.00	4.69
12	8.00	6.00



NOAA-NMFS,PACIFIC ENVIRONMENTAL GROUP, MONTEREY, CALIFORNIA

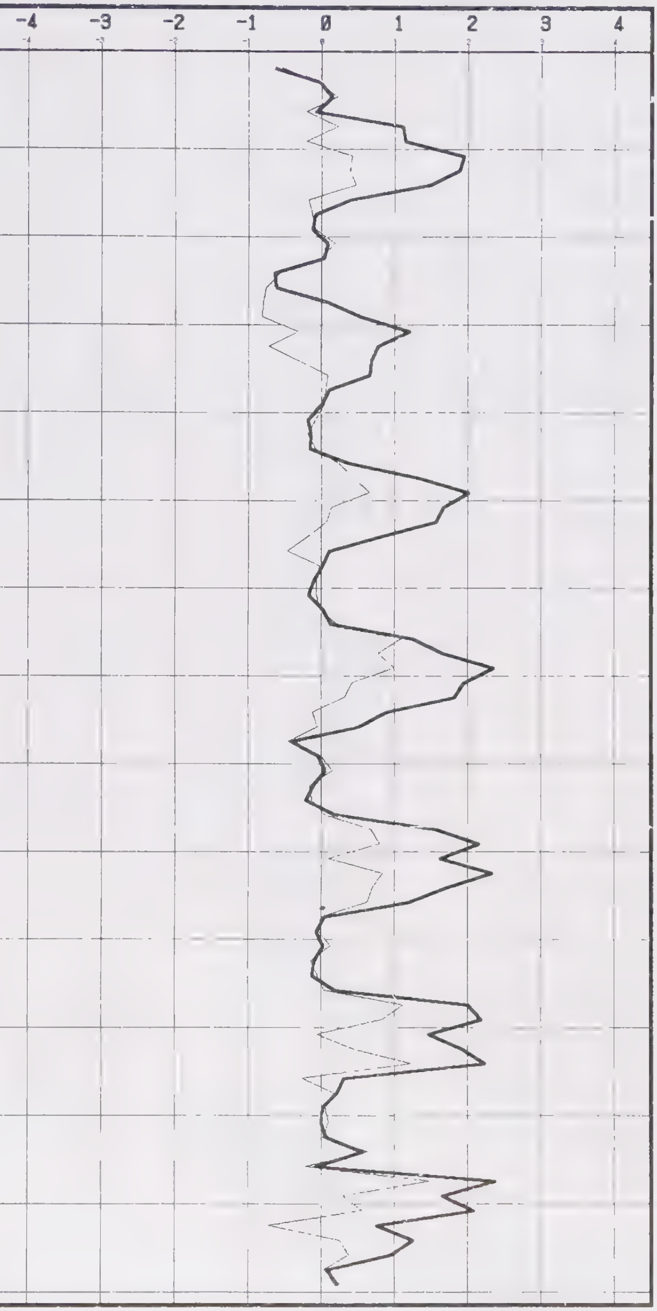
SVERDRUP TRANSPORT BY MONTH

MONTH	VALUE	ANOMALY
196301	.07	.19
2	0.00	-.04
3	-.12	-.04
4	-.82	-.96
5	-.28	-1.16
6	1.13	-.22
7	.56	-.96
8	1.13	-.35
9	.03	-.97
10	-.02	-.59
11	0.00	-.04
12	-.08	-.04
196401	-.13	-.02
2	.62	.58
3	.19	.27
4	.58	.44
5	-.66	-1.54
6	.46	-.89
7	1.07	-.45
8	1.15	-.33
9	1.21	.21
10	.25	-.32
11	-.01	-.05
12	-.49	-.45
196501	-.18	-.07
2	.37	.33
3	.04	.12
4	-.03	-.17
5	1.83	.95
6	.31	-1.04
7	.67	-.85
8	.72	-.76
9	.36	-.64
10	.27	-.30
11	-.18	-.22
12	-.03	.01
196601	-.15	-.04
2	-.16	-.20
3	-.65	-.57
4	.77	.63
5	.22	-.66
6	1.17	-.18
7	.09	-1.43
8	.86	-.62
9	.29	-.71
10	.64	.08
11	-.08	-.12
12	-.13	-.09
196701	-.07	.04
2	.38	.34
3	-.75	-.67
4	-1.10	-1.24
5	.66	-.22
6	.92	-.43
7	1.68	.16
8	1.46	-.02
9	.82	-.18
10	.58	.02
11	.11	.07
12	.14	.18
196801	.02	.14
2	-.13	-.17
3	-.31	-.23
4	1.22	1.08
5	-.46	-1.34
6	1.27	-.08
7	.81	-.71
8	.07	-1.42
9	.77	-.23
10	.33	-.24
11	-.26	-.30
12	-.12	-.08
196901	-.12	-.01
2	-.30	-.34
3	.12	.20
4	-.33	-.47
5	.85	-.03
6	.45	-.90
7	2.92	1.40
8	3.55	2.07
9	1.48	.48
10	.33	-.24
11	.60	.56
12	-.01	.03



SVERDRUP TRANSPORT BY MONTH

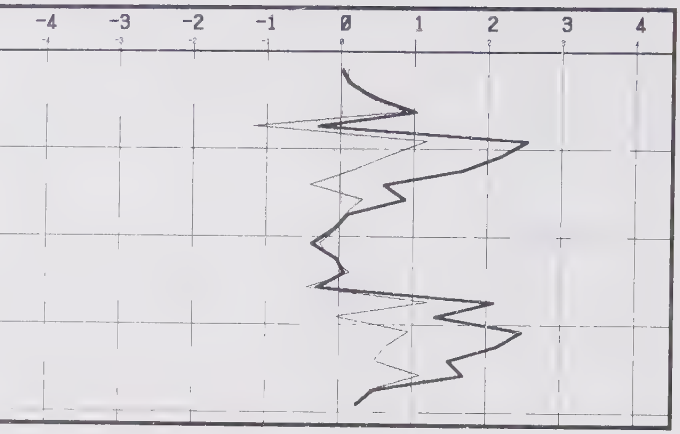
MONTH	VALUE	ANOMALY
197001	-.66	-.55
2	-.02	-.06
3	.14	.22
4	-.07	-.21
5	1.11	.23
6	1.14	-.21
7	1.94	.42
8	1.88	.40
9	1.47	.47
10	.39	-.18
11	-.09	-.13
12	-.13	-.09
197101	.08	.20
2	.03	-.01
3	-.65	-.57
4	-.62	-.76
5	.08	-.80
6	.54	-.81
7	1.20	-.32
8	.77	-.71
9	.68	-.32
10	.66	.10
11	.10	.06
12	0.00	.04
197201	-.19	-.08
2	-.15	-.19
3	-.16	-.08
4	.38	.24
5	1.33	.45
6	2.01	.66
7	1.66	.14
8	1.56	.08
9	.81	-.19
10	.10	-.47
11	.01	-.03
12	-.11	-.07
197301	-.18	-.07
2	.02	-.02
3	.13	.21
4	1.24	1.10
5	1.66	.78
6	2.35	1.00
7	1.94	.42
8	1.81	.33
9	.88	-.12
10	.51	-.05
11	-.42	-.46
12	-.05	-.01
197401	.04	.16
2	-.12	-.16
3	-.22	-.14
4	.18	.04
5	1.56	.68
6	2.15	.80
7	1.62	.10
8	2.33	.85
9	1.70	.70
10	1.19	.63
11	.04	-.00
12	-.07	-.03
197501	.02	.14
2	-.10	-.14
3	-.13	-.05
4	.18	.04
5	2.00	1.12
6	2.18	.83
7	1.46	-.06
8	1.92	.44
9	2.23	1.23
10	.30	-.27
11	.21	.17
12	.01	.05
197601	-.01	.11
2	.06	.02
3	.56	.64
4	-.08	-.22
5	2.37	1.49
6	1.65	.30
7	2.08	.56
8	.75	-.73
9	1.25	.25
10	.95	.39
11	.08	.04
12	.21	.25



NOAA-NMFS.PACIFIC ENVIRONMENTAL GROUP. MONTEREY, CALIFORNIA

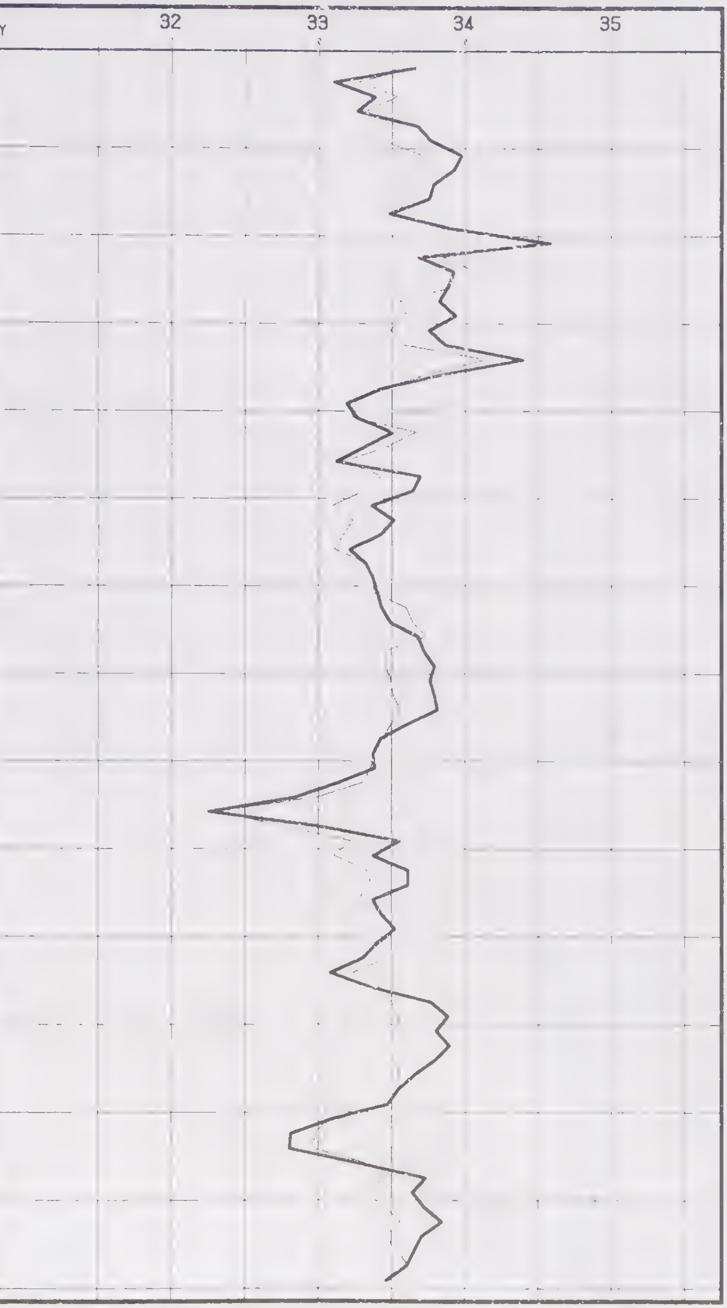
SVERDRUP TRANSPORT BY MONTH

MONTH	VALUE	ANOMALY
197701	0.00	.12
2	.12	.08
3	.43	.51
4	1.02	.88
5	-.30	-1.18
6	2.53	1.18
7	2.18	.66
8	1.66	.18
9	.59	-.41
10	.88	.32
11	.11	.07
12	-.08	-.04
197801	-.38	-.27
2	-.05	-.09
3	.06	.14
4	-.31	-.45
5	2.09	1.21
6	1.30	-.05
7	2.47	.95
8	2.14	.66
9	1.48	.48
10	1.68	1.12
11	.47	.43
12	.24	.28



SALINITY PACIFIC GROVE, CA BY MONTH

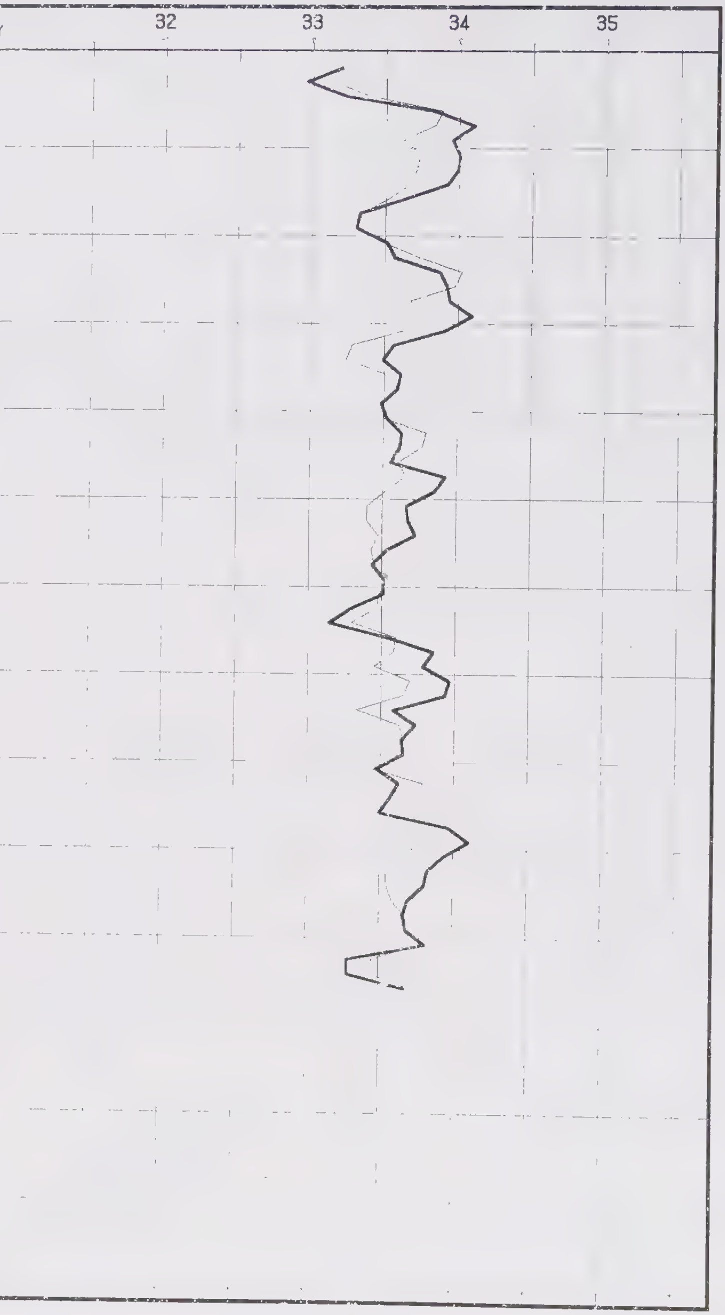
MONTH	VALUE	ANOMALY
196301	33.67	.15
2	33.10	-.23
3	33.38	.03
4	33.26	-.19
5	33.67	-.09
6	33.76	-.07
7	33.97	.20
8	33.92	.14
9	33.78	.03
10	33.75	.14
11	33.48	-.01
12	33.89	.40
196401	34.58	1.06
2	33.68	.35
3	33.92	.57
4	33.88	.43
5	33.82	.06
6	33.93	.10
7	33.75	-.02
8	33.86	.08
9	34.39	.64
10	33.85	.24
11	33.42	-.07
12	33.19	-.30
196501	33.26	-.26
2	33.50	.17
3	33.31	-.04
4	33.12	-.33
5	33.69	-.07
6	33.64	-.19
7	33.36	-.41
8	33.51	-.27
9	33.42	-.33
10	33.21	-.40
11	33.32	-.17
12	33.37	-.12
196601	33.40	-.12
2	33.43	.10
3	33.49	.14
4	33.68	.23
5	33.72	-.04
6	33.79	-.04
7	33.76	-.01
8	33.79	.01
9	33.81	.06
10	33.60	-.01
11	33.42	-.07
12	33.37	-.12
196701	33.38	-.14
2	33.13	-.20
3	32.84	-.51
4	32.25	-1.20
5	33.01	-.75
6	33.55	-.28
7	33.37	-.40
8	33.61	-.17
9	33.61	-.14
10	33.37	-.24
11	33.43	-.06
12	33.52	.03
196801	33.40	-.12
2	33.30	-.03
3	33.08	-.27
4	33.36	-.09
5	33.76	-.00
6	33.88	.05
7	33.80	.03
8	33.89	.11
9	33.79	.04
10	33.65	.04
11	33.54	.05
12	33.47	-.02
196901	33.09	-.43
2	32.81	-.52
3	32.80	-.55
4	33.26	-.19
5	33.73	-.03
6	33.64	-.19
7	33.72	-.05
8	33.84	.06
9	33.70	-.05
10	33.65	.04
11	33.60	.11
12	33.46	-.03



NOAA-NMFS.PACIFIC ENVIRONMENTAL GROUP, MONTEREY, CALIFORNIA

SALINITY PACIFIC GROVE, CA BY MONTH

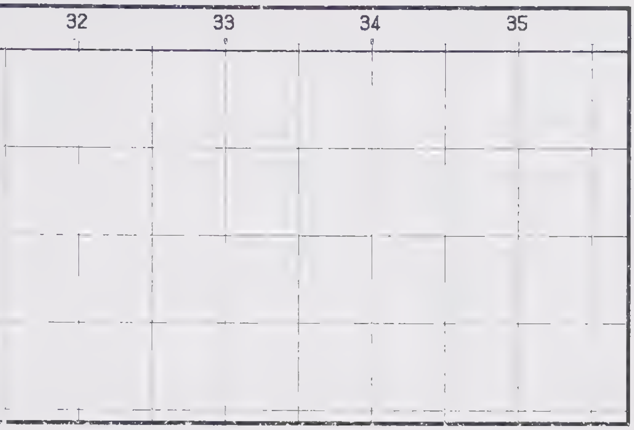
MONTH	VALUE	ANOMALY
197001	33.21	-.31
2	32.96	-.37
3	33.23	-.12
4	33.83	.38
5	34.10	.34
6	33.95	.12
7	34.00	.23
8	33.99	.21
9	33.92	.17
10	33.63	.02
11	33.32	-.17
12	33.30	-.19
197101	33.51	-.01
2	33.56	.23
3	33.87	.52
4	33.92	.47
5	33.94	.18
6	34.09	.26
7	33.91	.14
8	33.56	-.22
9	33.49	-.26
10	33.61	.00
11	33.59	.10
12	33.48	-.01
197201	33.52	-.00
2	33.62	.29
3	33.61	.26
4	33.55	.10
5	33.92	.16
6	33.85	.02
7	33.66	-.11
8	33.67	-.11
9	33.72	-.03
10	33.53	-.08
11	33.43	-.06
12	33.51	.02
197301	33.51	-.01
2	33.29	-.04
3	33.14	-.21
4	33.54	.09
5	33.65	.09
6	33.78	-.05
7	33.96	.19
8	33.93	.15
9	33.58	-.17
10	33.73	.12
11	33.64	.15
12	33.65	.16
197401	33.47	-.05
2	33.62	.29
3	33.56	.21
4	33.49	.04
5	33.96	.20
6	34.10	.27
7	33.93	.16
8	33.82	.04
9	33.80	.05
10	33.69	.08
11	33.66	.17
12	33.68	.19
197501	33.81	.29
2	33.78	-.05
3	33.28	-.07
4	33.57	.72
5	NO DATA	
6	NO DATA	
7	NO DATA	
8	NO DATA	
9	NO DATA	
10	NO DATA	
11	NO DATA	
12	NO DATA	
197601	NO DATA	
2	NO DATA	
3	NO DATA	
4	NO DATA	
5	NO DATA	
6	NO DATA	
7	NO DATA	
8	NO DATA	
9	NO DATA	
10	NO DATA	
11	NO DATA	
12	NO DATA	



NOAA-NMFS, PACIFIC ENVIRONMENTAL GROUP, MONTEREY, CALIFORNIA

SALINITY PACIFIC GROVE, CA BY MONTH

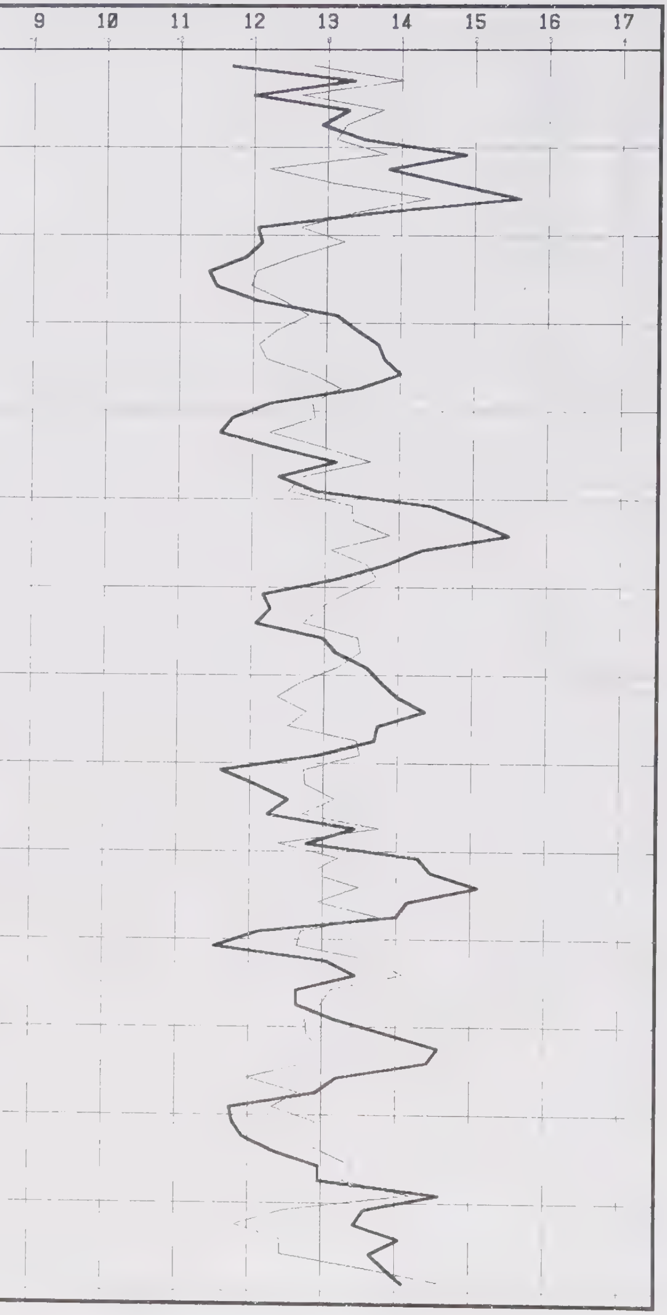
MONTH	VALUE	ANOMALY
197701	NO DATA	
2	NO DATA	
3	NO DATA	
4	NO DATA	
5	NO DATA	
6	NO DATA	
7	NO DATA	
8	NO DATA	
9	NO DATA	
10	NO DATA	
11	NO DATA	
12	NO DATA	
197801	NO DATA	
2	NO DATA	
3	NO DATA	
4	NO DATA	
5	NO DATA	
6	NO DATA	
7	NO DATA	
8	NO DATA	
9	NO DATA	
10	NO DATA	
11	NO DATA	
12	NO DATA	



NOAA-NMFS,PACIFIC ENVIRONMENTAL GROUP, MONTEREY, CALIFORNIA

SST PACIFIC GROVE, CA BY MONTH

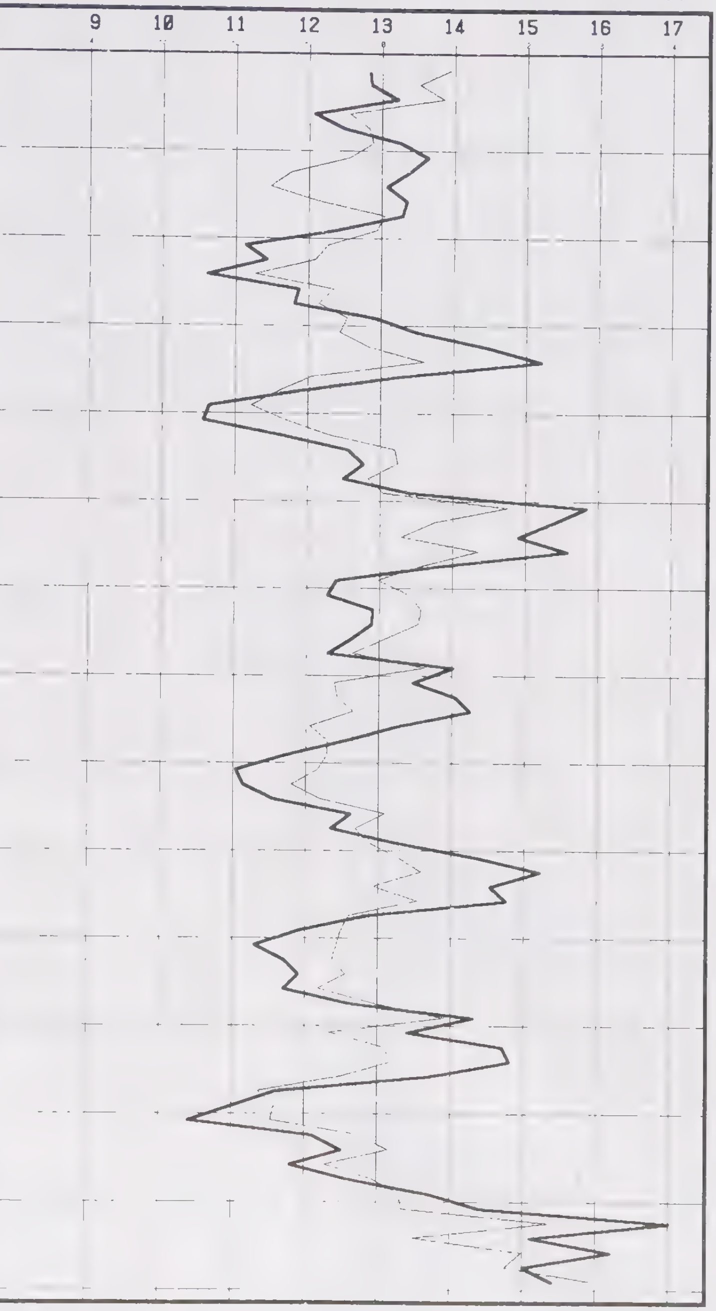
MONTH	VALUE	ANOMALY
196301	11.66	-.21
2	13.35	1.02
3	11.99	-.36
4	13.28	.76
5	12.92	.26
6	13.50	.12
7	14.87	.80
8	13.83	-.79
9	14.70	.10
10	15.61	1.40
11	13.61	.37
12	12.05	-.37
196401	12.11	.24
2	11.90	-.43
3	11.39	-.96
4	11.49	-1.03
5	12.06	-.60
6	13.13	-.25
7	13.40	-.67
8	13.70	-.92
9	13.78	-.82
10	14.00	-.21
11	13.44	.20
12	12.23	-.19
196501	11.72	-.15
2	11.56	-.77
3	12.30	-.05
4	13.13	.61
5	12.36	-.30
6	12.87	-.51
7	14.44	.37
8	15.00	.38
9	15.48	.88
10	14.30	.09
11	13.81	.57
12	13.13	.71
196601	12.15	.28
2	12.25	-.08
3	12.06	-.29
4	12.97	.45
5	13.15	.49
6	13.57	.19
7	13.76	-.31
8	13.98	-.64
9	14.36	-.24
10	13.72	-.49
11	13.68	.44
12	12.91	.49
196701	11.60	-.27
2	12.08	-.25
3	12.51	.16
4	12.23	-.29
5	13.42	.76
6	12.77	-.61
7	14.28	.21
8	14.45	-.17
9	15.09	.49
10	14.14	-.07
11	13.99	.75
12	12.12	-.30
196801	11.52	-.35
2	13.03	.70
3	13.44	1.09
4	12.64	.12
5	12.64	-.02
6	13.15	-.23
7	13.86	-.21
8	14.56	-.06
9	14.41	-.19
10	13.19	-1.02
11	12.91	-.33
12	11.74	-.68
196901	11.78	-.09
2	11.92	-.41
3	12.34	-.01
4	12.95	.43
5	12.95	.29
6	14.58	1.20
7	13.57	-.50
8	13.43	-1.19
9	14.04	-.56
10	13.65	-.56
11	13.86	.62
12	14.09	1.67



NOAA-NMFS, PACIFIC ENVIRONMENTAL GROUP, MONTEREY, CALIFORNIA

SST PACIFIC GROVE, CA BY MONTH

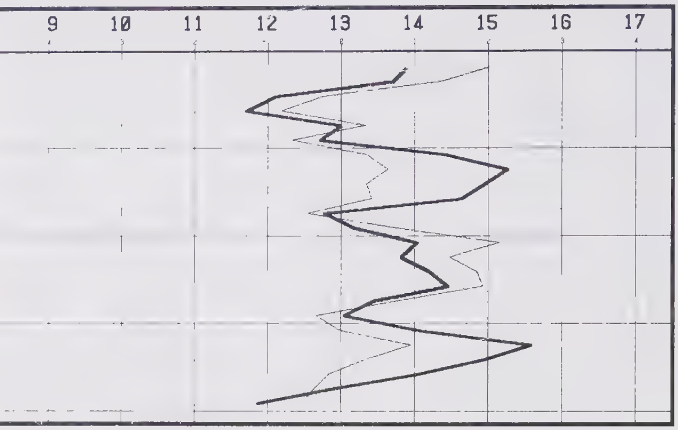
MONTH	VALUE	ANOMALY
197001	12.83	.96
2	12.85	.52
3	13.21	.86
4	12.07	-.45
5	12.48	-.18
6	13.26	-.12
7	13.63	-.44
8	13.38	-1.24
9	13.07	-1.53
10	13.34	-.87
11	13.28	.04
12	12.35	-.07
197101	11.13	-.74
2	11.42	-.91
3	10.61	-1.74
4	11.86	-.66
5	11.80	-.86
6	12.91	-.47
7	13.50	-.57
8	14.46	-.16
9	15.20	.60
10	13.26	-.95
11	11.83	-1.41
12	10.64	-1.78
197201	10.56	-1.31
2	11.61	-.72
3	12.55	.20
4	12.76	.24
5	12.49	-.17
6	13.42	.04
7	15.83	1.76
8	15.38	.76
9	14.90	.30
10	15.57	1.36
11	13.83	.59
12	12.40	-.02
197301	12.28	.41
2	12.90	.57
3	12.89	.54
4	12.61	.09
5	12.29	-.37
6	14.01	.63
7	13.46	-.61
8	14.04	-.58
9	14.24	-.36
10	13.26	-.95
11	12.53	-.71
12	11.71	-.71
197401	11.03	-.84
2	11.13	-1.20
3	11.55	-.80
4	12.61	.09
5	12.34	-.32
6	13.24	-.14
7	14.34	.27
8	15.21	.59
9	14.53	-.07
10	14.75	.54
11	12.83	-.41
12	11.91	-.51
197501	11.30	-.57
2	11.70	-.63
3	11.90	-.45
4	11.70	-.82
5	12.60	-.06
6	14.30	.92
7	13.40	-.67
8	14.70	.08
9	14.80	.20
10	13.70	-.51
11	11.60	-1.64
12	11.00	-1.42
197601	10.40	-1.47
2	12.10	-.23
3	12.50	.15
4	11.80	-.72
5	12.60	-.06
6	13.70	.32
7	14.40	.33
8	17.00	2.38
9	15.10	.50
10	16.20	1.99
11	15.00	1.76
12	15.40	2.98



NOAA-NMFS, PACIFIC ENVIRONMENTAL GROUP, MONTEREY, CALIFORNIA

SST PACIFIC GROVE, CA BY MONTH

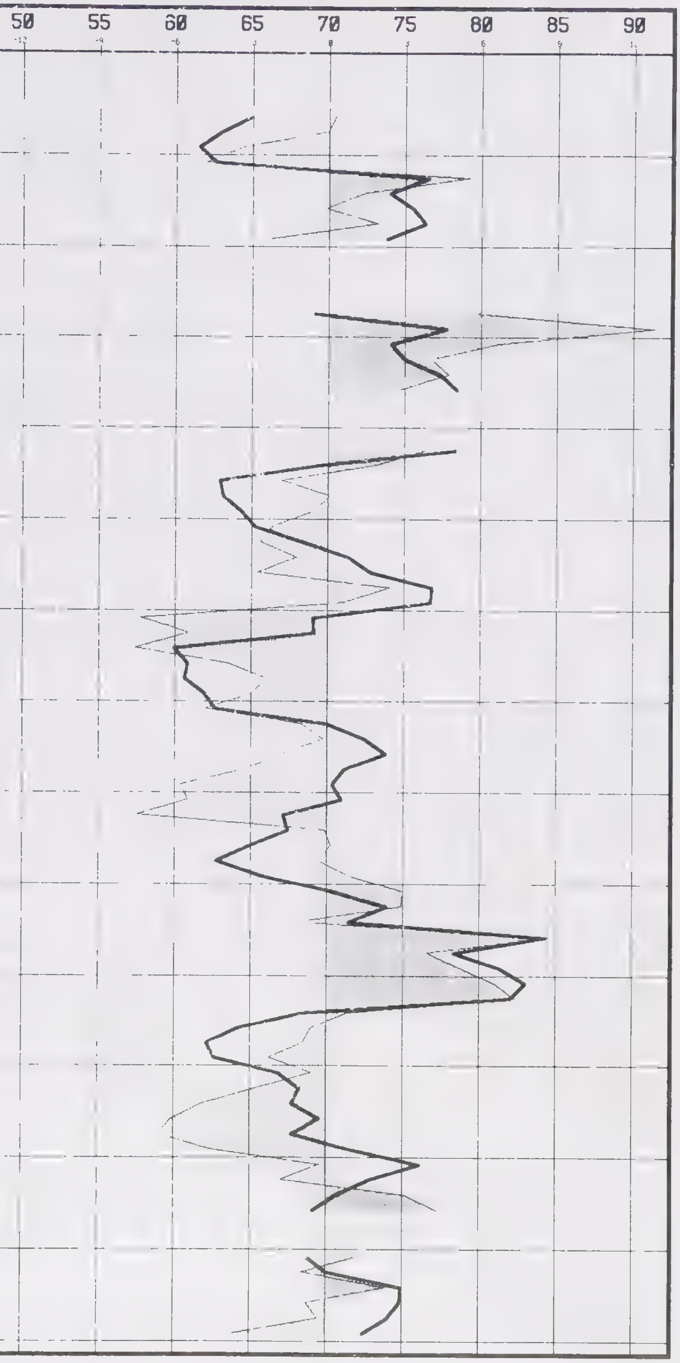
MONTH	VALUE	ANOMALY
197701	13.90	2.03
2	13.70	1.37
3	12.10	-.25
4	11.70	-.82
5	13.00	.34
6	12.71	-.67
7	14.42	.35
8	15.26	.64
9	14.95	.35
10	14.63	.42
11	12.77	-.47
12	13.18	.76
197801	14.03	2.16
2	13.81	1.48
3	14.20	1.85
4	14.45	1.93
5	13.43	.77
6	13.04	-.34
7	14.04	-.03
8	15.58	.96
9	14.94	.34
10	14.04	-.17
11	12.87	-.37
12	11.86	-.56



NOAA-NMFS, PACIFIC ENVIRONMENTAL GROUP, MONTEREY, CALIFORNIA

CM DYNAMIC HEIGHT BY MONTH

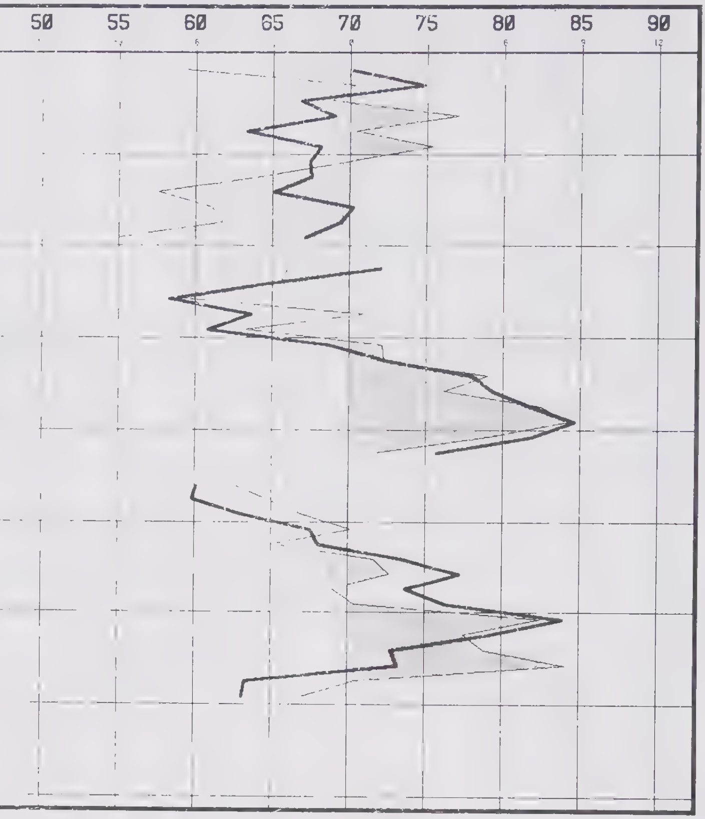
MONTH	VALUE	ANOMALY
196801	NO DATA	
196802	NO DATA	
196803	NO DATA	
196804	65.00	.26
196805	63.00	-.04
196806	61.50	-3.37
196807	62.60	-4.80
196808	76.50	5.54
196809	74.00	1.43
196810	75.50	-.08
196811	76.30	1.96
196812	73.80	-2.26
196901	NO DATA	
196902	NO DATA	
196903	NO DATA	
196904	NO DATA	
196905	68.90	5.86
196906	77.70	12.83
196907	74.10	6.70
196908	75.00	4.04
196909	77.30	4.73
196910	78.40	2.82
196911	NO DATA	
196912	86.60	10.54
197001	NO DATA	
197002	78.52	3.91
197003	69.40	1.90
197004	62.90	-1.84
197005	63.10	.06
197006	64.30	-.57
197007	65.20	-2.20
197008	68.30	-2.66
197009	71.30	-1.27
197010	72.80	-2.78
197011	76.60	2.46
197012	76.70	.64
197101	69.00	-7.39
197102	69.10	-5.49
197103	59.90	-7.60
197104	60.80	-3.94
197105	60.60	-2.44
197106	61.90	-2.97
197107	62.60	-4.80
197108	69.90	-1.05
197109	72.40	-.17
197110	73.60	-1.78
197111	71.10	-3.24
197112	70.30	-5.76
197201	70.90	-5.43
197202	67.10	-7.49
197203	67.40	-.10
197204	64.90	.16
197205	62.70	-.34
197206	65.70	.83
197207	76.40	3.00
197208	73.90	2.94
197209	71.40	-1.17
197210	84.30	8.72
197211	78.30	3.95
197212	81.30	5.24
197301	83.00	6.61
197302	82.00	7.41
197303	68.30	.80
197304	64.10	-.64
197305	62.10	-.94
197306	62.60	-2.27
197307	66.80	-.62
197308	68.20	-2.76
197309	67.70	-4.87
197310	69.50	-6.08
197311	67.70	-6.64
197312	71.50	-4.55
197401	76.10	-.29
197402	72.80	-1.79
197403	70.60	3.10
197404	69.10	4.36
197405	NO DATA	
197406	NO DATA	
197407	68.70	1.30
197408	70.00	-.96
197409	74.90	2.33
197410	74.80	-.78
197411	74.00	-.34
197412	72.40	-3.66



NOAA-NMFS, PACIFIC ENVIRONMENTAL GROUP, MONTEREY, CALIFORNIA

CM DYNAMIC HEIGHT BY MONTH

MONTH	VALUE	ANOMALY
197501	70.00	-6.39
197502	74.80	.21
197503	66.80	-.70
197504	69.00	4.26
197505	63.30	.26
197506	68.10	3.23
197507	67.40	.00
197508	67.50	-3.46
197509	65.10	-7.47
197510	70.20	-5.38
197511	69.40	-4.94
197512	67.10	-8.96
197601	NO DATA	
197602	72.20	-2.39
197603	64.80	-2.70
197604	58.30	-6.44
197605	63.60	.56
197606	60.80	-4.07
197607	66.70	1.30
197608	72.30	1.34
197609	78.00	5.43
197610	79.30	3.72
197611	81.80	7.46
197612	84.60	8.54
197701	81.80	5.41
197702	75.70	1.11
197703	NO DATA	
197704	60.10	-4.64
197705	59.80	-3.24
197706	63.00	-1.87
197707	67.50	.10
197708	68.00	-2.96
197709	73.60	1.03
197710	77.20	1.62
197711	73.70	-.64
197712	76.30	.24
197801	83.90	7.51
197802	79.10	4.51
197803	72.80	5.30
197804	73.20	8.46
197805	63.30	.20
197806	63.10	-1.77
197807	NO DATA	
197808	NO DATA	
197809	NO DATA	
197810	NO DATA	
197811	NO DATA	
197812	NO DATA	



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Lipid and Fatty Acid Composition of the Endogenous Energy Sources of Striped Bass *(Morone saxatilis)* Eggs

MAXWELL B. ELDRIDGE[a,*], **JEANNE D. JOSEPH**[b], **KAREN M. TABERSKI**[a] and **GLORIA T. SEABORN**[b], [a] *Southwest Fisheries Center, Tiburon Laboratory, National Marine Fisheries Service, 3150 Paradise Drive, Tiburon, CA 94920, and* [b] *Southeast Fisheries Center, Charleston Laboratory, National Marine Fisheries Service, PO Box 12607, Charleston, SC 29412*

ABSTRACT

The unique physiological flexibility of the early life stages of striped bass is attributed to the calorie-rich endogenous energy sources of the striped bass egg. Eggs of different aged striped bass from geographically separate populations were examined for lipid and fatty acid compositions and were found to be basically similar. Yolk components of the eggs contained significantly less total lipid than oil globules, were more diverse in lipid class composition and consisted mostly of polar lipids. Oil globules were entirely lipid material consisting predominantly of steryl/wax esters. Fatty acid compositions of yolk and oil globules differed according to their respective lipid compositions. The functional significance of these lipids is discussed in relation to the ecological context of the early life stages.

Lipids 18:510-513, 1983.

INTRODUCTION

Studies on the feeding ecology and bioenergetics of striped bass embryos and larvae have indicated that early life stages are able to endure long periods of starvation and that they lack a critical period, defined as the sensitive and brief time when larvae begin active feeding and must convert from endogenous to exogenous energy sources (1,2). This physiological flexibility is largely attributed to the egg oil globule which persists for extended periods through the embryonic into the larval stage. At fertilization, the striped bass egg is characterized by a large single oil globule which comprises 55% of the total egg weight and 71% of the total caloric content. Proteinaceous yolk (5600 cal g^{-1}) and the oil globule (9500 cal g^{-1}) combine to an average 2.04 calories per egg. Lipid stores of the striped bass egg are of interest not only for their physiological and ecological functions, but also because they serve as reservoirs for lipophilic contaminants.

The following report presents information on the lipid and fatty acid compositions of the yolk and oil globule components of fully mature striped bass eggs. The object of our study was to further understanding of the physiology of the early life stages of striped bass by providing a detailed description of their initial lipid stores.

MATERIALS AND METHODS

Specimen Collection and Preparation

Five sexually mature striped bass were collected from the San Francisco Bay/Delta estuary and 2 females from the Coos River in Oregon. California fish were younger (5 and 6 yr) and smaller (62.4 cm mean standard length) than those from Oregon (8 and 14 yr; 78.5 cm standard length) such that fecundities also differed (0.6 vs 1.8 million eggs per female for California and Oregon, respectively). Subsamples of the left ovary ($\sim$150 g wet weight) were quick-frozen and stored at −40 C until analyzed. Eggs were removed from the center of each ovary, homogenized and centrifuged to separate yolk and oil globule components. The yolk and oil layers were aspirated into separate containers and lipids extracted from each fraction by the chloroform/methanol extraction procedure of Bligh and Dyer (3).

Prior to lipid analysis samples were stripped of solvent and ca. 50 mg of yolk or oil lipid was weighed and dissolved in 1 ml $CHCl_3$. This solution, or appropriate dilutions, was used for thin layer chromatography (TLC), quantitative analysis of lipid classes by TLC with flame ionization detection (FID) and gas liquid chromatography (GLC).

Thin Layer Chromatography/Flame Ionization Detection

Lipid classes present in the yolk and oil samples were separated and identified by comparison with a standard mixture on Silica Gel G plates (Supelco, Bellefonte, PA) developed in hexane/diethyl ether/acetic acid (80:20:1) and visualized with iodine and by spraying with 5% molybdophosphoric acid in 95% ethanol. A second plate, spotted and developed in the same manner, was sprayed with Liebermann-Burchard reagent after development, to confirm the presence of steryl esters.

Quantitation of individual lipid classes was achieved by TLC/FID. A comprehensive description of this relatively new technique is given by Ackman (4). An Iatroscan TH-10 analyzer was used with an Omniscribe B-5000 dual pen strip

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[*] To whom correspondence should be addressed.

chart recorder. The FID was operated with a hydrogen flow rate of 160 ml/min and air flow rate of 2000 ml/min. Chromarods (type SII) were spotted with ca. 20 μg of lipid in $CHCl_3$ solution and developed in hexane/diethyl ether/formic acid (85:15:0.02). Following development, the rods were dried at 110 C for 4 min and scanned at a rate of 0.42 cm/sec. Peak areas were measured with a stepping pen integrator and were converted to weight percent lipid class by the use of correction factors (5,6) derived from authentic lipid standards. Steryl esters (SE) and wax esters (WE) could not be separated by the solvent system described above nor by any of the several other solvent mixtures attempted and are therefore reported as a sum.

Gas Liquid Chromatography

Methyl esters of fatty acids of all yolk and oil samples were prepared using 14% boron trifluoride in methanol, following saponification with 0.5 N potassium hydroxide. Esters were extracted with hexane and purified by TLC prior to GLC analysis. Fatty acid methyl esters were separated isothermally at 210 C on a Quadrex fused silica wall coated open tubular column (50 m×0.21 mm id) coated with Carbowax 20-M operated in a Hewlett-Packard 5830 gas chromatograph equipped with an FID. Helium was used as the carrier gas at a flow of 1.5 ml/min (60 psig). Individual methyl ester peaks were provisionally identified using pure standards, secondary standards and equivalent chain length calculations. Relative composition was obtained by area normalization directly from the Hewlett-Packard 18850A terminal. Aliquots of the methyl esters were hydrogenated and rechromatographed to ensure the accuracy of identification of major components and to confirm that there was no significant loss of polyunsaturates during GLC.

RESULTS AND DISCUSSION

Lipid Composition

The high total lipid content of the egg was largely attributable to the oil globule. Yolk, which comprised an average 38% of the egg dry weight, contained 3.8% total lipids, while the oil globule was 100% extractable lipids. Eggs of other fishes, even those with distinct oil globules, have been found to have significantly less total lipid contents than eggs from striped bass (7-10). For example, a survey of eggs from 6 species by Kaitaranta and Ackman (10) showed total lipids to vary 2.4-9.2%.

Lipid classes differed sharply between egg yolk and oil globule components (Table 1), thus confirming that our technique successfully separated yolk and oil globule lipids. Only wax and steryl esters and triacylglycerols were present in the oil globules with steryl and wax esters averaging 90.4% of the total lipids. This is also the major lipid found in some marine zooplankton, particularly arctic upper-water crustacea (11,12). The presence of wax esters in fish is documented mostly in somatic tissues (muscle and liver) of deep-water forms (13-15). The occurrence of steryl/wax esters in eggs is ecologically more diverse (10), including marine and freshwater species: *Mugil cephalus* (16), *Merluccius capensis, Theragra chalcogramma,* and *Scomber japonicus* (17), *Trichogaster cosby* (18), *Perca fluviatilis, Lota lota* (19), and *Sciaenops ocellati* (7). We suspected wax esters were in striped bass eggs because Dergaleva and Shatunovskiy (20) had found declining concentrations of this lipid class in larvae and juveniles of striped bass from 8 to 40 days after hatching. An important morphological feature common to eggs of all these species is the presence of discrete oil globules.

Although yolk lipids comprised a small portion of the yolk weight, it was more diverse in its composition than oil globule lipids. Phospholipids were an average 78.9% of yolk total lipids. This is not unusual since phospholipids are documented as the major lipid of egg yolks in a variety of fishes (10,19,21-23). Yolk is the endogenous energy source first consumed by the embryo and larvae (1), and is totally absorbed within 5 days after hatching (at 18 C), a period characterized by extensive tissue differentiation and growth. Since phospholipids are the major lipid constituents of biomembranes, it seems logical they were preferentially transferred

TABLE 1

Lipid Class Composition (Percent) of Oil Globules and Yolk Lipids of Striped Bass Eggs[a]

Egg component	Steryl and wax esters	Triacylglycerols	Free fatty acids	Sterols	Phospholipids
Yolk	5.3 ± 1.7	6.5 ± 1.9	6.6 ± 1.8	2.8 ± 0.9	78.9 ± 2.9
Oil globule	90.4 ± 2.8	9.6 ± 2.8	---	---	---

[a] Values presented as means ± standard errors for all fish combined, 4 determinations per fish.

from the yolk during this period. Free fatty acids and sterols were also present in small quantities and, like phospholipids, were present only in the yolk. The varying amounts of free fatty acids were probably due to hydrolysis of the samples during storage or laboratory work-up. Sterols were most likely cholesterol, which is common to most animal tissues.

Fatty Acid Composition

Fish lipids are generally characterized by high contents of long-chain polyunsaturated fatty acids. Such was the case with both striped bass yolk and oil globule lipids (Table 2). The dominant isomers of the C_{18} to C_{20} monoethylenic fatty acids were the 18:1ω9 and 20:1ω9 reported elsewhere for fish lipids (24). The respective fatty acid composition of yolk and oil globule lipids basically reflected differences in their lipid classes. The fatty acid composition of the yolk lipids was typical of marine phospholipids being dominated by palmitic (16:0), eicosapentaenoic (20:5ω3) and docosahexaenoic (22:6ω3) acids. Oil globule lipids were made up of fatty acids very similar to those found in somatic tissues of meso- and bathypelagic fishes, animals known to often have large amounts of wax esters (14,25). The principal acids were oleic (18:1ω9), palmitoleic (16:1ω7) and docosahexaenoic (22:6ω3). Egg lipids of striped bass from this study had a mixed fatty acid composition which is indicative of overlapping freshwater and marine environments (26). Total C_{16} and C_{18} fatty acids were high; palmitic acid was high in the yolk and the tetraenoic acids low. The lack of a clear pattern agrees with the life history of the species, namely, that it inhabits the estuarine zone.

The fatty acid composition was also consistent among individual females regardless of location, age, condition or pollutant burden. Lasker and Theilacker (27) also found remarkably similar fatty acid patterns among sardine eggs of different females at different stages of maturation.

The functional roles of high lipid contents and steryl/wax esters in fish embryos and larvae have not been determined, but it may be proposed that they generally serve in marine organisms for metabolic energy or buoyancy (28). Their most clearly identified purpose is in providing energy, especially in situations of food deprivation (15,25,29), emergencies of delayed hatch (30), or when large reserves of energy are needed for rapid embryonic development (7). In the context of the early life stage ecology of striped bass, the unique lipid characteristics serve to provide: (a) abundant energy for rapid embryonic development (incubation period = 48 hr at 18 C); (b) necessary flotation of pelagic eggs and early larvae until formation of functional swim bladders; and (c) long-term energy for feeding larvae because of uncertainty of food availability (e.g., dietary zooplankton patchiness).

TABLE 2

Fatty Acid Composition of Yolk and Oil Globule Components of Striped Bass Eggs[a]

Fish fatty acids	Yolk	Oil globule
Saturates		
14:0	1.2 ± 0.1	1.6 ± 0.4
16:0	17.5 ± 1.9	6.2 ± 0.6
18:0	9.9 ± 0.9	0.7 ± 0.2
Monoenes		
16:1ω9	1.3 ± 0.2	2.2 ± 0.4
16:1ω7	4.6 ± 0.5	13.8 ± 1.6
18:1ω9	15.5 ± 1.8	35.7 ± 2.7
18:1ω7	4.2 ± 0.4	5.4 ± 0.6
20:1ω11	trace	0.3 ± 0.4
20:1ω9	1.2 ± 0.3	1.1 ± 0.2
20:1ω7	0.1 ± 0.0	0.1 ± 0.1
Dienes		
18:2ω6	0.8 ± 0.3	1.8 ± 0.6
20:2ω6	0.2 ± 0.1	0.2 ± 0.0
Trienes		
18:3ω3	0.2 ± 0.1	0.7 ± 0.2
20:3ω6	0.1 ± 0.0	0.1 ± 0.0
Tetraenes		
18:4ω3	0.3 ± 0.1	0.8 ± 0.3
20:4ω3	0.2 ± 0.1	0.6 ± 0.1
20:4ω6	3.3 ± 0.4	1.3 ± 0.3
22:4ω6	0.3 ± 0.3	trace
Pentaenes		
20:5ω3	8.6 ± 3.8	6.4 ± 1.6
22:5ω6	0.2 ± 0.1	0.3 ± 0.1
22:5ω3	2.4 ± 0.7	2.9 ± 0.7
Hexaenes		
22:6ω3	19.9 ± 2.2	10.0 ± 1.5

[a] Percent composition by weight presented as means ± standard error.

The occurrence of discrete oil globules in fish eggs and larvae is more common than one might think. In a worldwide review of fish egg surveys, Ahlstrom and Moser (31) found that most pelagic marine fish eggs have discrete oil globules. As the oil globules of these and inshore and estuarine species are analyzed, we believe that steryl/wax esters will be found to be the principal form of endogenous energy in the eggs.

Recent findings show that striped bass eggs from geographically distant populations contained high levels of petrochemicals, pesticides and chlorinated hydrocarbons (32) which correlated with reduced reproductive capacity and lowered early life stage survival. The advantages of lipid to the embryo and larva are then offset by the facility with which lipophilic and toxic chemicals are accumulated from the environment.

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SATELLITE REMOTE SENSING OF THE HABITAT OF SPAWNING ANCHOVY IN THE SOUTHERN CALIFORNIA BIGHT

PAUL C. FIEDLER
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038

ABSTRACT

Images of sea-surface temperature and phytoplankton pigments in the Southern California Bight were processed from satellite data obtained during four intensive CalCOFI anchovy egg surveys from 1980 to 1982. Mesoscale patterns of water masses and fronts in the images can explain the distribution of northern anchovy spawning as indicated by first-day eggs. In general, spawning in the northwestern region of the bight is excluded from a cold-water mass south of Point Conception, whereas spawning to the south is confined to coastal waters with moderately high phytoplankton pigment levels. The satellite-measured parameters may indicate critical factors for larval survival. Such satellite images can be used to improve the sampling efficiency of egg surveys.

RESUMEN

Mediante satélites se han obtenido imágenes de la temperatura de la superficie del mar y de pigmentos del fitoplancton, para la zona del seno del sur de California. Estos datos han sido procesados conjuntamente con la información obtenida durante cuatro exploraciones de CalCOFI (1980-1982) para recolectar huevos de anchoa (*Engraulis mordax*).

El contorno de la distribución de masas de agua y frentes en estas imágenes, puede informar sobre la distribución de la actividad de puesta de la anchoa, señalada por la presencia de huevos de un dia en las colecciones. En general, la puesta en la parte noroeste del seno está aislada de la masa de aguas frías al sur de Punta Concepción, mientras que la zona de puesta al sur está confinada a las aguas costeras con niveles relativamente elevados de pigmentos fitoplanctónicos.

Los parámetros medidos por el satélite pueden ser indicadores de factores críticos para la supervivencia de las larvas. Las imágenes proporcionadas por los satélites podrían utilizarse para perfeccionar la eficacia en el muestreo de huevos de anchoa.

INTRODUCTION

Intensive anchovy egg surveys of the CalCOFI region inshore of station 60 have been conducted once or twice yearly since 1980. The Southern California Bight (Figure 1) is the center of distribution of the large central stock of northern anchovy and has been sampled most intensively. The spatial distribution of early stage eggs, indicating recent spawning, corresponds closely to the distribution of adults in night midwater trawls during the spawning season (Figure 2). Temperature and salinity were the only environmental parameters measured routinely on these surveys, although nutrients, phytoplankton pigments, and primary productivity have been measured on some CalCOFI cruises. Vertical egg tows were made at stations 7.4 km apart on transect lines separated by 37 km. This sampling plan gives considerably higher resolution of spatial distribution patterns than does the regular 37- (74-)km CalCOFI station (line) spacing.

Sensors carried on earth-orbiting satellites since 1978 provide high-resolution images of sea-surface temperature and phytoplankton pigment concentration. Accurate estimates of these parameters, corrected for atmospheric scattering and absorption, can be derived from multispectral radiance data. Temperature data are derived from the thermal infrared channels of the Advanced Very High Resolution Radio-

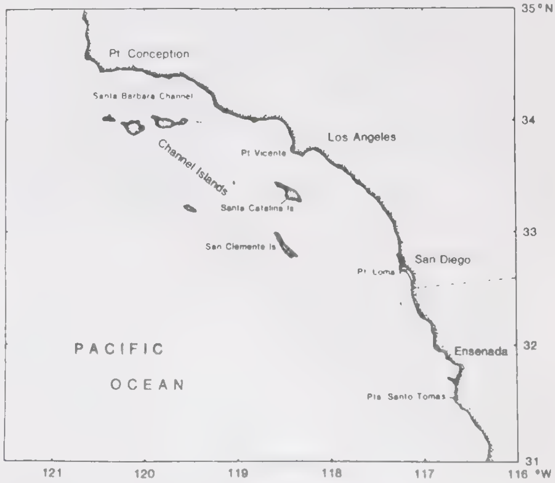

Figure 1. Map of the Southern California Bight.

[Manuscript received February 25, 1983.]

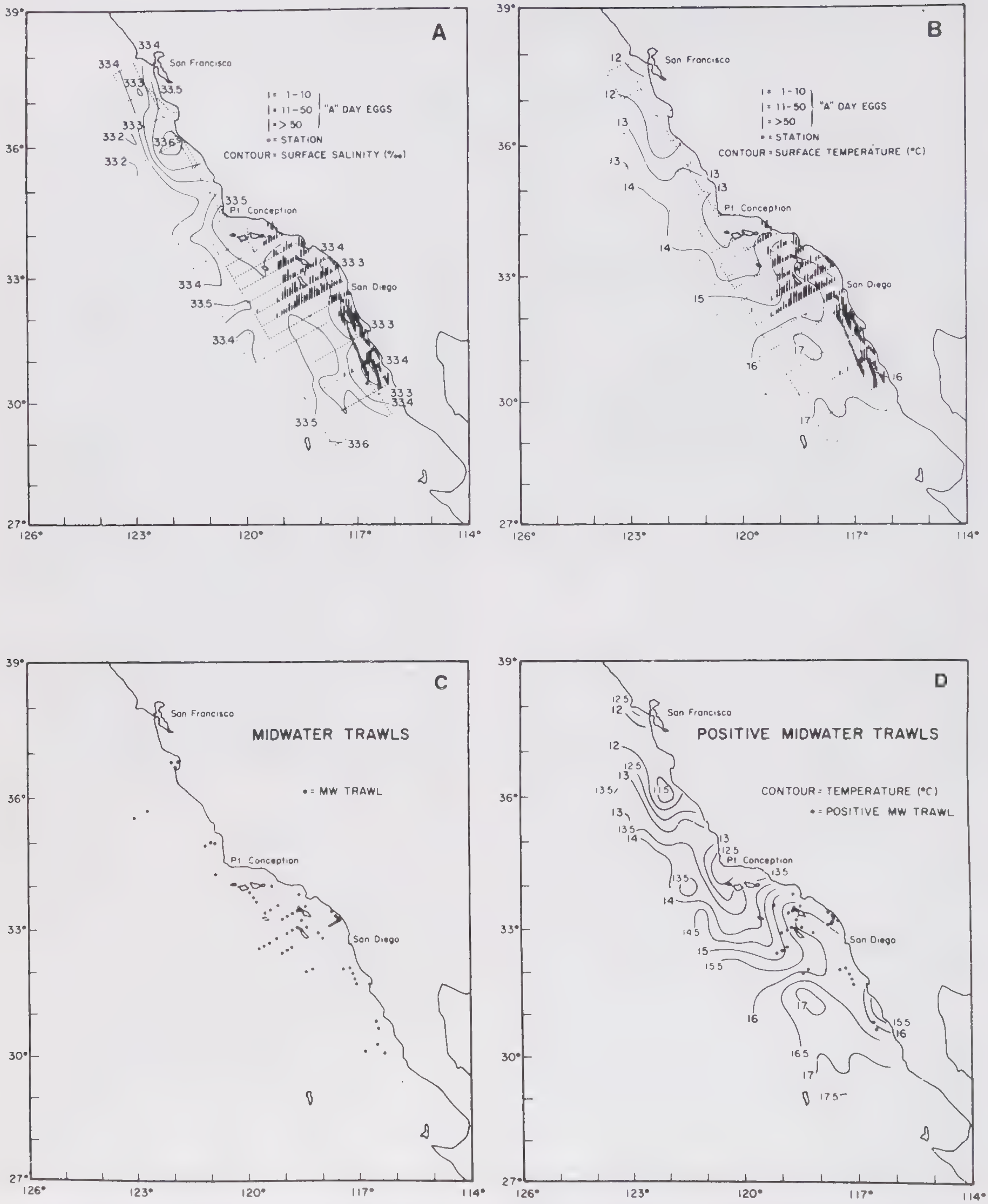

Figure 2. Distribution of anchovy eggs and adults in relation to salinity and temperature, CalCOFI cruise 8003: (*A*) A-day eggs and surface salinity; (*B*) A-day eggs and surface temperature; (*C*) all midwater trawls taken from March 27 to April 12, 1980, by R/V *David Starr Jordan;* (*D*) midwater trawls with adult anchovy catches and surface temperature. From Lasker et al. (1981).

TABLE 1
1980-82 CalCOFI Egg Survey Dates and Stations in the Southern California Bight, and Dates and Times of Corresponding AVHRR and CZCS Images

CalCOFI cruise	Southern California Bight stations		AVHRR image	CZCS image
	Dates	N		
8003	20 Mar-10 Apr 1980	359	7 Apr, 1850 PST	8 Apr, 1113 PST
8004	12 Apr-29 Apr 1980	286	—	—
8102	16 Feb- 6 Mar 1981	429	21 Feb, 1955 PST	23 Feb, 1124 PST
8104	31 Mar-12 Apr 1981	373	5 Apr, 2029 PST	4 Apr, 1144 PST
8202	27 Jan-27 Feb 1982	543	29 Jan, 1334 PST	29 Jan, 1109 PST

meter (AVHRR) currently on NOAA-7 and formerly on TIROS-N and NOAA-6. Phytoplankton pigment data are derived from the visible channels of the Coastal Zone Color Scanner (CZCS) on Nimbus-7.

Synoptic images of California coastal waters obtained daily or twice daily and with a resolution of ~1 km give us a much different view of the CalCOFI survey region than is provided by a ship taking hydrographic samples at 37-km intervals on a month-long cruise. This report demonstrates that satellite images define environmental features and boundaries on a scale that helps explain the spatial patterns of spawning activity observed on intensive egg surveys in the Southern California Bight.

DATA AND METHODS

Five intensive egg surveys were completed in 1980-82 (Table 1). Anchovy eggs from vertical egg tows (333-μm-mesh conical net of 25-cm diameter from a depth of 70 m for 1 min) were sorted and staged. Net tows were standardized so that sample counts are equivalent to eggs per 0.05 m^2. Counts of A-day eggs (0-24 hours old) were assumed to represent recent spawning at the station location. Positive egg stations were sorted by egg count into three classes of approximately equal size.

AVHRR infrared data were obtained for the most cloud-free day during each survey, from satellite passes archived at the Scripps Satellite Oceanography Facility (SSOF). Radiance data were converted to temperature using an SSOF radiometric calibration procedure based on Lauritson et al. (1979). Correction for atmospheric water vapor and aerosols, without concomitant sea-truth or atmospheric data, is possible using empirical regressions of ship temperatures on satellite temperatures in two or three thermal infrared bands. The NOAA-6 AVHRR had only two such channels, and the 3.7-μm channel was plagued by excessive noise that steadily increased during the operational lifetime of the satellite. Two-channel correction of the full-resolution NOAA-6 images (8003, 8102, and 8104) was therefore not possible. The 8202 image was corrected with a "split-window" algorithm[1] using channels 4 (10.9μm) and 5 (12.0μm) of the NOAA-7 AVHRR.

Ship-bucket temperatures, obtained at egg tow stations on the same day as the satellite pass, were used to correct the NOAA-6 images. Additive corrections for cold biases of −1.87°, −1.96°, and −1.77°C in the 8003, 8102, and 8104 images yielded root-mean-square differences of 0.50°, 0.52°, and 0.32°C ($n=27$, 16, and 32 stations). Since corrections based upon linear regression of ship temperatures on satellite temperatures produced only slight improvements (rms differences = 0.36°, 0.32°, and 0.32°C), the simple additive correction was used. Removal of a residual bias of −0.18°C from the corrected 8202 image yielded an rms difference of 0.23°C ($n=35$).

The Visibility Laboratory of Scripps Institution of Oceanography performed preliminary processing of CZCS data. Band 1 (blue) and band 3 (yellow-green) radiances were corrected for Rayleigh and aerosol scattering by Visibility Lab versions of the CZCS Nimbus Experimental Team's atmospheric algorithm (Smith and Wilson 1981). This algorithm was modified between the dates when the 8003 and 8102 images were processed. The 8104 image was corrected only for Rayleigh scattering, but there was little aerosol contamination visible in the corrected image. Blue/green ratios were converted to phytoplankton pigment concentration (chlorophyll plus phaeopigments) with the pigment algorithm of Smith and Baker (1982). Absolute levels of phytoplankton pigments in the images presented here are not comparable because of the application of different atmospheric correction algorithms and the lack of sea-truth data.

RESULTS

Frequency distributions of ship-bucket temperature measured at stations in the Southern California Bight, and the percentage of positive stations in each temperature interval, are illustrated in Figure 3. Little or no spawning occurred at stations <13.5°C. The warmest

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[1] McClain, E. P. 1981. Split-window and triple-window sea surface temperature measurements from satellites. Preprint. Mini-symposium on Applications of Aerospace Remote Sensing in Marine Research. ICES Statutory Meeting, Woods Hole, Mass., 6-10 October 1981.

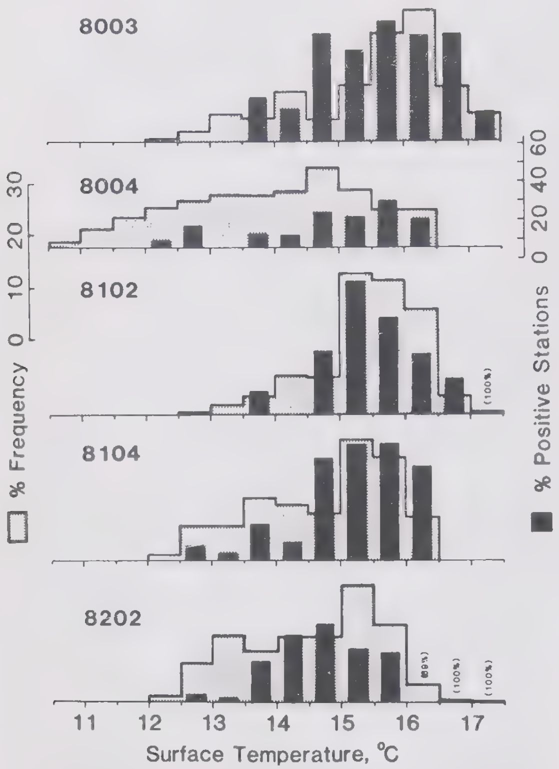

Figure 3. Frequency distributions of CalCOFI stations by surface temperature, and frequency of positive A-day anchovy egg catches within each temperature interval, for five intensive egg surveys. Large percentages of small numbers of stations are in parentheses. Only stations within the Southern California Bight, from line 80 to line 101.6 and no farther offshore than station 60, were included. Extra transects added on cruise 8202 were omitted.

mean surface temperature was observed on cruise 8003 (15.2°C), when spawning occurred most frequently at 14.5-17°C. Mean temperature decreased to 14.4°C during cruise 8004. Spawning was reduced considerably, with eggs found at only 29 of 286 bight stations, and this cruise will not be considered further.

Mean surface temperatures on cruises 8102 (15.1°C) and 8104 (14.7°C) were slightly lower than on 8003, but the modal temperature range of successful spawning did not change. The 1982 egg survey was earlier in the year than 8003 and 8102. Mean surface temperature in the bight was only 14.3°C. The modal spawning temperature range was about 0.5°C colder than in 1980 and 1981, whereas the frequency of successful spawning within that range was generally lower.

The satellite images are enhanced so that low temperatures and high phytoplankton pigment levels appear light, while high temperatures and low pigment levels appear dark. All four pairs of images (Figures 4-7) show the same basic mesoscale features:

1. A plume of cold water upwelled off Point Conception and to the north, and then advected to the south by the California Current. This water has relatively high phytoplankton pigment concentrations.
2. A narrow band of cool water caused by local upwelling along the coast to the east and south of the plume. Occasionally, small plumes extend farther offshore from prominent capes such as Point Vicente, Point Loma, and Punta Santo Tomás. This water has moderately high phytoplankton pigment concentrations.
3. A mass of warm, low-pigment oceanic water extending from the south between the cold-water plume and the coast.

Variations between and within years can be seen in the intensity and size of the mesoscale features and in the detailed shape of frontal boundaries along the coast and around the large cold-water plume. Sea-surface temperature and phytoplankton pigment patterns are somewhat coherent, with an inverse relationship between the two parameters.

8003 (Figure 4a,b)

The cold-water plume defines a boundary on the distribution of spawning activity north of San Clemente Island. The boundary corresponds to approximately the 14.5°C isotherm. Spawning was confined to a 40-km-wide band near the coast south of San Diego. There was no obvious temperature boundary defining this band, although the water offshore was relatively warm (16-17°C). Spawning has been commonly observed in 17-19°C water off Baja California during spring CalCOFI cruises in 1969-79, and Lasker et al. (1981) attributed the offshore absence of spawning in this case to the slightly higher salinity of this warm-water pool (0.1-0.2°/oo; see Figure 1). The phytoplankton pigment image, however, reveals a much more obvious boundary. Spawning is limited to a coastal band of relatively high-pigment water south of San Diego.

8102 (Figure 5a,b)

The cold-water plume at this time extended more to the south than to the southeast, as it did during cruise 8003. Spawning was excluded from the plume north of Santa Catalina Island, although some spawning did occur in relatively cool water in the Santa Barbara Channel (13.5-14°C). Phytoplankton pigment levels from the CZCS were higher than during 8003, a difference that may be due partly to changes in the atmospheric correction algorithm. Although there is

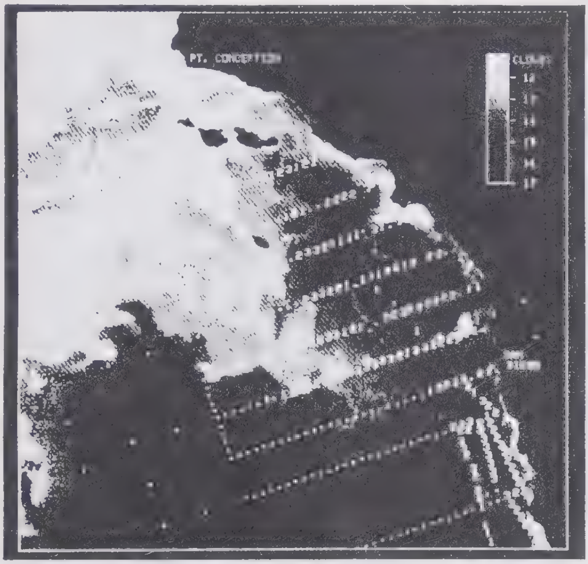

Figure 4a. CalCOFI 8003 A-day anchovy egg distribution, March 20-April 10, 1980. • = 0, 1 = 1-4, 2 = 5-17, 3 = 18-245 eggs/0.05 m^2. Sea-surface temperature (°C) from NOAA-6 AVHRR, channel 4, April 7, 1980.

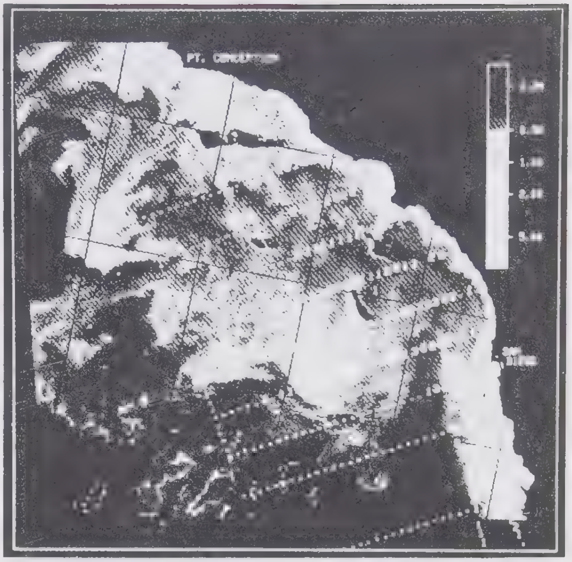

Figure 4b. CalCOFI 8003 A-day anchovy egg distribution, March 20-April 10 1980. • = 0, 1 = 1-4, 2 = 5-17, 3 = 18-245eggs/0.05m ^{2}. Phytoplankton pigments (mg m $^{-3}$) from Nimbus-7 CZCS, April 8, 1980

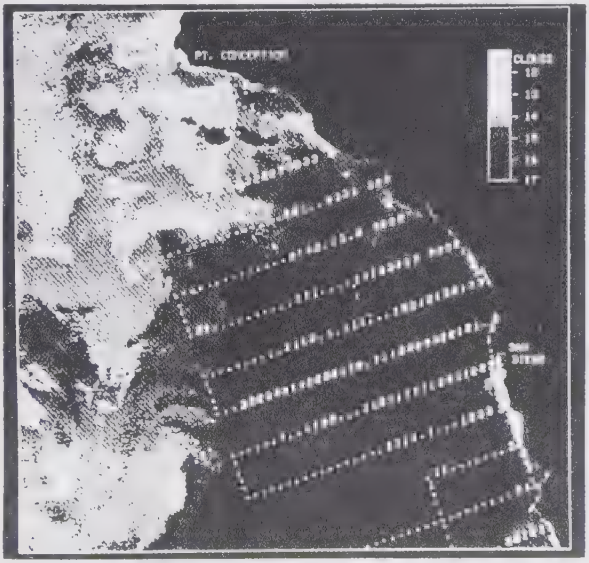

Figure 5a CalCOFI 8102 A-day anchovy egg distribution, February 12-March 10, 1981. • = 0, 1 = 1-4, 2 = 5-15, 3 = 16-157 eggs/0.05 m^2 Sea-surface temperature (°C) from NOAA-6 AVHRR, channel 4, February 21, 1981

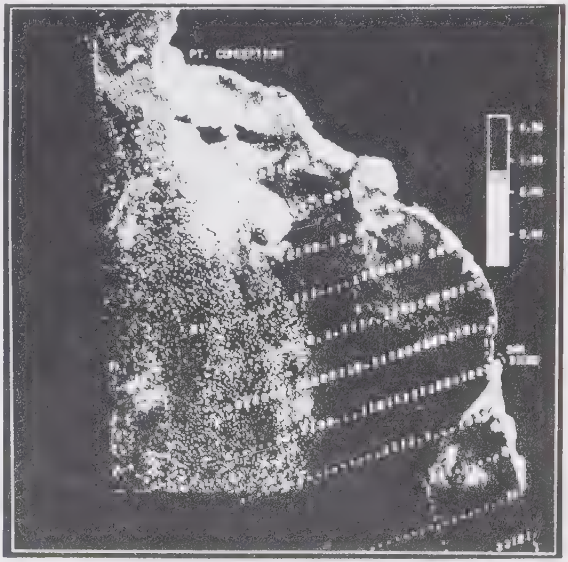

Figure 5b. CalCOFI 8102 A-day anchovy egg distribution, February 12 March 10, 1981. • = 0, 1 = 1-4, 2 = 5-15, 3 = 16-157 eggs/0.05 m^2 Phytoplankton pigments (mg m^{-3}) from Nimbus-7 CZCS, February 23, 1981

no absolute lower limit on the distribution of spawning apparent in the satellite phytoplankton-pigment image, higher egg abundances south of Santa Catalina Island tended to occur at stations with higher pigment levels ($r = +0.23$, $P = <0.018$, product-moment correlation of log-transformed values).

8104 **(Figure 6a,b)**

Temperatures were generally colder than during 8102, and the cold-water plume extended farther east among the Channel Islands. Spawning did not extend as far to the northwest, although an isolated pocket of spawners remained in the cool Santa Barbara Channel.

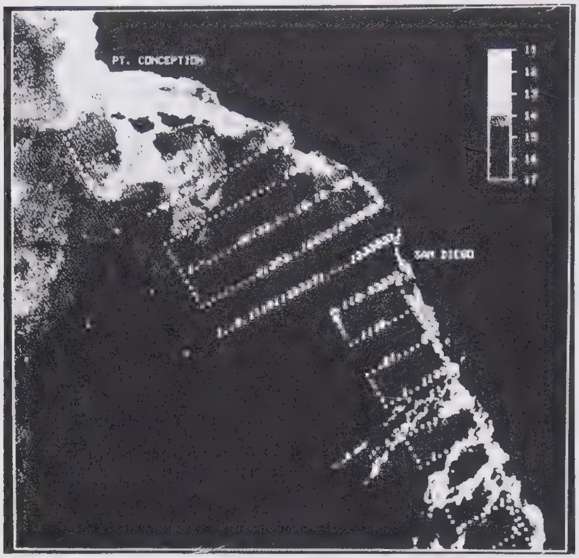

Figure 6a. CalCOFI 8104 A-day anchovy egg distribution, March 31-April 12, 1981. • = 0, 1 = 1-4, 2 = 5-13, 3 = 14-323 eggs/0.05 m². Sea-surface temperature (°C) from NOAA-6 AVHRR, channel 4, April 5, 1981.

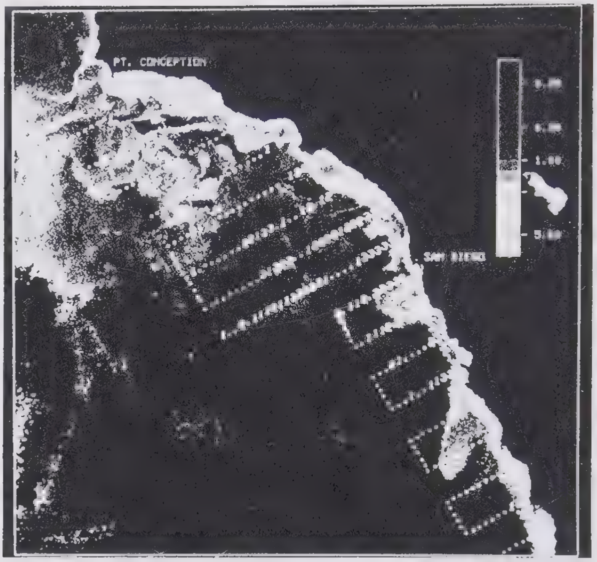

Figure 6b. CalCOFI 8104 A-day anchovy egg distribution, March 31-April 12, 1981. • = 0, 1 = 1-4, 2 = 5-13, 3 = 14-323 eggs/0.05 m². Phytoplankton pigments (mg m^{-3}) from Nimbus-7 CZCS, April 4, 1981.

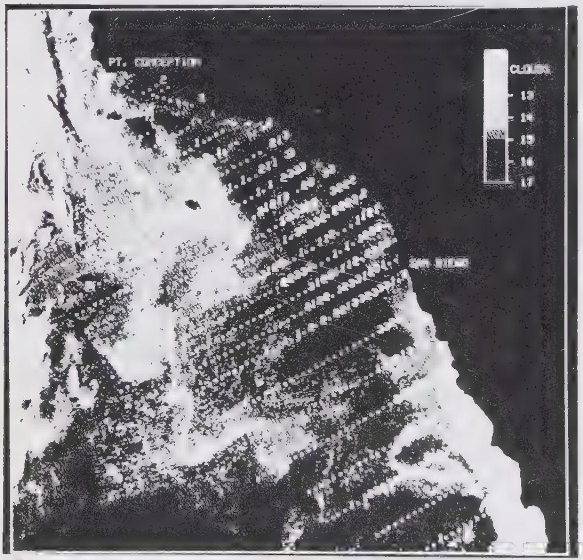

Figure 7a. CalCOFI 8202 A-day anchovy egg distribution, January 27-February 27, 1982. • = 0, 1 = 1-3, 2 = 4-12, 3 = 13-170 eggs/0.05 m². Sea-surface temperature (°C) from NOAA-7 AVHRR, channels 4 and 5, February 18, 1982.

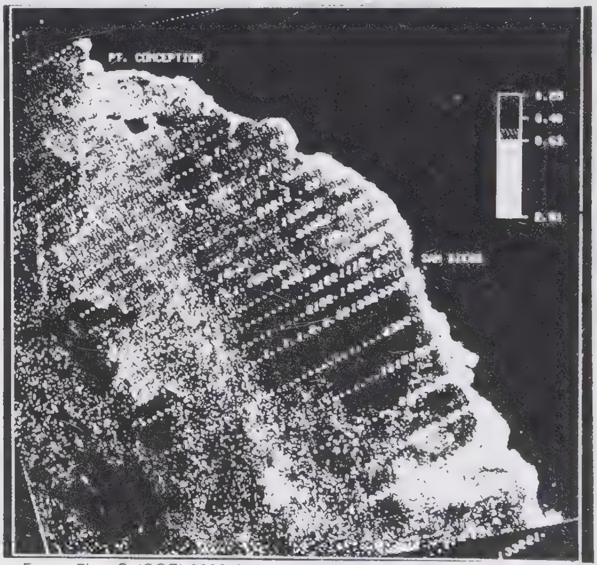

Figure 7b. CalCOFI 8202 A-day anchovy egg distribution, January 27-February 27, 1982. • = 0, 1 = 1-3, 2 = 4-12, 3 = 13-170 eggs/0.05 m². Phytoplankton pigments (mg m^{-3}) from Nimbus-7 CZCS, January 29, 1982

More spawning occurred south of San Diego, especially in high-pigment waters near the coast.

8202 **(Figure 7a,b)**

Sampling was intensified between lines 83.3 and 95.0 on this survey, with transects separated by 18.5 km. The cold-water plume once again formed a definite boundary on the northwestern extent of spawning activity. To the south, spawning was confined near the coast except off Punta Santo Tomás, south of Ensenada, where a plume of cool water with high phytoplankton pigment levels extended far offshore.

DISCUSSION AND CONCLUSIONS

The satellite images reveal mesoscale and smaller patterns of sea-surface temperature and phytoplankton pigments that define boundaries on northern anchovy spawning in the Southern California Bight. While neither parameter alone is sufficient, both together may define the spatial distributions nearly completely. In general, the northern extent of spawning in the bight, and the offshore extent north of Santa Catalina Island, are limited by cold, upwelled water advected south of Point Conception. Spawning activity to the south is limited by low phytoplankton pigment levels in oceanic water found 20-100km offshore, rather than by temperature.

During cruise 8003, spawning did not occur in water $<14°C$ or <0.2 mg pigments m^{-3} (Figure 8A). At higher temperature and phytoplankton pigment levels, spawning was apparently limited by an interaction, in that the lower temperature limit decreased as pigment concentration increased. A similar relationship holds for cruise 8102 (Figure 8B), although a lower phytoplankton pigment limit was not observed. Note, however, that no eggs were found at many stations with temperature and pigment concentrations within the ranges in which spawning occurred at other stations.

Surface temperature and phytoplankton pigment concentration cannot, therefore, be the only factors determining the distribution of spawning activity. In fact, they may merely indicate more directly important environmental conditions. Spawning in waters favorable for larval survival is an adaptive strategy in the life cycle of many species of fish (Cushing 1975). Lasker (1981) hypothesized that the survival of first-feeding anchovy larvae depends upon the aggregation of nutritionally suitable food organisms in a stratified water column. Large dinoflagellates are preferred food organisms often found in dense near-surface layers in the Southern California Bight.

Satellite observations of relatively warm surface temperatures along with moderately high pigment levels may indicate a stratified water column with a mature phytoplankton community dominated by dinoflagellates. On the other hand, a well-mixed water column would be indicated by colder surface temperatures caused by upwelling or storm mixing; unsuitable food conditions would be indicated either by the low phytoplankton pigment levels of unproductive oceanic water or by very high levels associated with surface diatom blooms in recently upwelled water.

Satellite images of temperature and phytoplankton pigments are "snapshots" of the surface waters of the anchovy environment. Although smaller-scale features change noticeably on time scales of a few days, mesoscale patterns in the Southern California Bight may change little during a 2- to 4-week CalCOFI egg survey (Bernstein et al. 1977). Therefore, satellite data can supplement a survey's environmental data by providing higher-resolution views of sea-surface temperature covering regions larger than the survey grid and by providing estimates of phytoplankton pigment concentrations not normally measured on the surveys. The images presented here demonstrate the utility of satellite data for interpreting spatial distributions from fishery surveys.

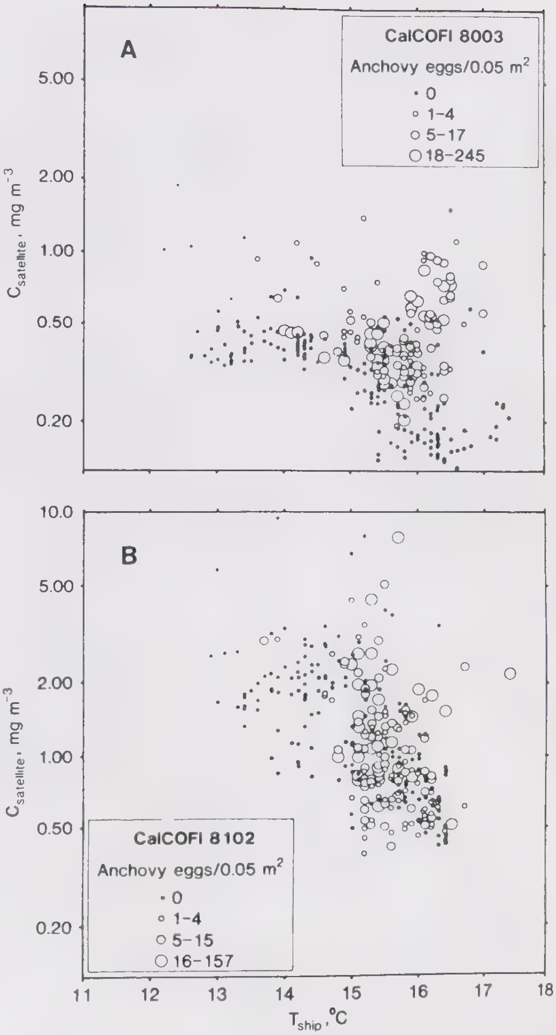

Figure 8. Anchovy A-day egg abundance vs ship-bucket temperature (T ship) and satellite chlorophyll (phytoplankton pigment) concentration. (*A*) Cruise 8003. (*B*) Cruise 8102.

Rapid collection and processing of satellite data allow real-time application in planning oceanographic cruises. The primary objective of CalCOFI egg surveys is to estimate anchovy spawning biomass for calculating optimum yield according to the Northern Anchovy Fishery Management Plan. The efficiency of these surveys could improve tremendously if satellite images were used to omit portions of the sampling grid where environmental conditions preclude spawning. This application is currently being explored, but will require a quantitive formulation of the relationships demonstrated here.

ACKNOWLEDGMENTS

I thank Michael Laurs for initiating and supporting my work with satellite imagery, also Reuben Lasker for providing data and encouragement, and Ruth Wittenberg and Roswell Austin of the Scripps Visibility Laboratory for processing and advising on the CZCS images. This work supported in part by NASA, order W15, 334.

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FEATURE ARTICLES

MARINE TURTLE STAMPS
-
PROMOTING CONSERVATION

Few people may realize that there are now some 175 postage stamps and souvenir sheets depicting 7 species of living marine turtles.

While the first of these stamps was issued nearly 50 years ago, almost half of them were produced within only the last 5 years. The green turtle (*Chelonia mydas*) and the hawksbill turtle (*Eretmochelys imbricata*) are, by far, the species most commonly depicted.

Whereas many of the older stamps portrayed sea turtles as secondary designs, most of the recent issues depict these animals prominently. It appears that many issuing countries are now using postage stamps to call attention to the endangered status of marine turtles. A few examples include Italy, the Maldives, Guyana, the Philippines, and Trinidad and Tobage. Whether or not sea turtle conservation was the immendiate purpose for the issues, the increase in the number of stamps is welcome news to those concerned with promoting the conservation of these animals. These stamps certainly make millions of people aware of the animals. This is an important first step in the conservation effort. The curious and concerned will make an effort to learn more about these subjects. However, the effort would greatly benefit from more publicity. Those with adequate knowledge and in a position to do so should write articles about sea turtles, whether for the pupular mass media or for the technical journals. In this way a wider public will be reached and conservation promoted.

For anyone concerned with sea turtle conservation, or involved with philately of stamp collecting, the following list of all known stamps depicting marine turtles should be of interest. The order of this list is alphabetical by country and chronologically within each issuing authority.
Dates of issues are provided, followed by catalog numbers according to Scott (American) and Stanley Gibbons (British). The denomination of the stamp is given in the next column. Next is the designation of the stamp in Scott's Catalog (1983), where listed, and finally the description printed on the stamp and/or our own notes in parentheses.

The Cayman Islands has issued nearly one-third of the stamps, and was the first to issue ones with marine turtles on them. The first dozen stamps featured Kings William IV and George V prominently and also show a small green turtle and a small hawksbill. The higher denominations of these stamps are now quite rare and consequently expensive. It should be noted that the Coat of Arms of the Cayman Islands includes a marine turtle and several stamps portray this emblem. The same is true for the Solomon Islands. As on this writing (March 1983) the most recent marine turtle stamps are from the Solomon Islands.

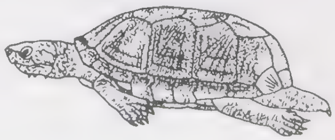
Some of the stamps show highly stylized marine turtles. Prominent among these are ones from French Polynesia, New Caledonia and Sarawak. Other unusual issues include stamps from Tuvalu and the Caymen Islands that bear coins engraved with marine turtles. A set of three stamps issued by Ascension in 1973 are the only ones with a triangular format. Both the Cayman Islands and the Solomon Islands have issued stamps showing marine turtles reprinted on another stamp.

The Maldive Islands has the distinction of being the only country to portray all seven species of sea turtles. No other country has depicted the flatback, *Chelonia depressa,* or Kemp's ridley, *Lepidochelys kempi,* on a stamp. The black turtle, *Chelonia agassizi,* which is sometimes considered as a separtate and eighth species, has never been shown on a stamp.

The utilitarian aspect of marine turtles is illustrated on several stamps. Two of these appear in Captain Cook Voyage series: Ascension and Gilbert Islands. Green turtles provided the famous explorer with food on parts of his long expeditions. The sole Cuban issue shows a turtle being pursued by a diver with a spear. One stamp of Dominica depicts a diver grasping a sea turtle. In this same vein, an issue from the Turks and Caicos Islands depicts a cartoon scene with the Disney character, Goofy, being pulled by a sea turtle.

Whereas the older stamps showed engravings of sea turtles in monochrome, the more recent issues as usually true-to-live colored images of the turtles. The identifications are alo generally accurate, but there are exceptions. The first Indonesian issue (1966) shows a hawksbill which is labeled *Chelonia mydas*. The second North Vietnam stamp (1975) labeled *Dermochelys coriacea* shows a turtle with a strange carapace not shaped like a leatherback. A 1977 stamp of Djibouti shows a hakwbill labeled as *Chelonia mydas*.

By and large, the stamps and souvenir sheets are interesting and attractive. The amateur collector can make a substantial collection without too much effort, since the majority of the stamps are relatively recent and inexpensive. The more serious collector will be challenged to find some of them, especially the reissues of several countries. Of course, only the ambitious and affluent can afford to complete the collection since the catalog value of the entire list runst into more than two thousand U.S. dollars.



LIST OF MARINE TURTLE STAMPS OF THE WORLD

By
Edgardo D. Gomez and George H. Balazs
March 1983

		Catalog No.				
Country	Date issued	Scott	Stanley Gibbons	Denomination	Description given in Scott	Wording on stamp and/or authors' brief description (in parentheses)
Anguilla	20 May 1975	160	144a	$10	Green-back turtle	(Turtle underwater)
	1976	246	240	$10	New Constitution 1976 No. 160 overprinted	"
Ascension	2 July 1934	24	22	1p	Map of Ascension	(Small stylized turtle)
	"	26	24	2p	"	"
	"	29	27	8p	"	"
	"	31	29	2 sh. 6p	"	"
	19 Nov. 1956	70	65	7p	Young green turtles	Young turtles (Two stylized turtles)
	28 Aug. 1973	170	171	4p	Green turtle	Chelonia mydas (Juvenile underwater--triangular stamp)
	"	171	172	9p	Loggerhead	Caretta caretta (Adult on a beach--triangular stamp)
	"	172	173	12p	Hawksbill	Eretmochelys imbricata (Adult underwater-triangular stamp)
	21 May 1978	229c	235	25p	Green turtle (in SS)	(Stylized in the shape of a bookend)
	8 Jan. 1979	237	244	12p	Green turtle	Chelonia mydas caught by Cook's crew on Ascension Island for nourishment (Adult underwater)
Bahamas	1971	316	362	4c	Hawksbill turtle (w/w 314)	(Juvenile underwater)
	21 Sept. 1971	318	364	6c	Hawksbill turtle (w/w 314)	"
	2 Nov. 1976	400	468	25c	Hawksbill turtle (w/w 173)	"
	June 1978	439	521	25c	Hawksbill turtle (no watermark)	"
	1979		468a	25c	Hawksbill turtle (chalk-surfaced paper)	"
Bermuda	19 Feb. 1979	378	402	$3	Green turtle	Chelonia mydas (Juvenile grazing on sea grass)
Cayman Islands	5 Dec. 1932	69	84	1/4p	King William IV, King George V	(Small stylized hawksbill and green turtle)
	"	70	85	1/2p	"	"
	"	71	86	1p	"	"
	"	72	87	1 1/2p	"	"
	"	73	88	2p	"	"
	"	74	89	2 1/2p	"	"
	"	75	90	3p	"	"
	"	76	91	6p	"	"
	"	77	92	1sh	"	"
	"	78	93	2sh	"	"
	"	79	94	5sh	"	"
	"	80	95	10sh	"	"
	1935-1936	90	105	2 1/2p	Hawksbill turtles	(5 turtles crawling down a beach)
	"	92	107	6p	"	"
	"	95	110	5sh	"	"
	5 May 1938	104a	119	2p	Hawksbill turtle (perf. 11.5 x 13)	(4 turtles crawling down a beach)
		107a	122	6p	"	"
		111	126	10sh	"	"
	16 July 1943	104	119a	2p	Hawksbill turtle (perf. 14)	"
		107	122a	6p	"	"
		111a	126a	10sh	"	"
	8 July 1947		122b	6p	Hawksbill turtle (perf. 11.5 x 13) (brownish olive)	"
	2 Oct. 1950	124	137	1p	Green turtle	(Unusual adult and 3 carapaces--King)
	"	131	144	1sh	Turtle "crawl"	Turtle in "crawl" (6 small turtles--King)
	7 July 1954	137	150	1p	Green turtle	(Same as Scott 124, but Queen)
	21 Feb. 1955	145	158	1sh	Turtle "crawl"	(Same as Scott 131, but Queen)
	6 Jan. 1959	149	161a	L1	Elizabeth II and turtles	(Small marine turtle carapace)
	4 July 1959	151	163	2 1/2p	Arms of Cayman Islands	(Stylized turtle in Coat of Arms)
		152	164	1sh	"	"

Country	Date issued	Catalog No.		Denomination	Description given in Scott	Wording on stamp and/or authors' brief description (in parentheses)
		Scott	Stanley Gibbons			
	28 Nov. 1962	159	171	4p	Green turtle	(Adult on a beach)
		166	178	10sh	Coat of Arms	(Stylized turtle)
	1 Dec. 1967	194	206	6p	Skin diving	(Juvenile by scuba diver)
	5 June 1969	223	235	10sh	Coat of Arms	(Stylized turtle)
	8 Sept. 1969	240	251	$1 on 10sh	"	"
	8 Sept. 1970	275	286	$1	"	"
	28 Jan. 1971	284	295	7c	Green turtle	Chelonia mydas (Adult on a beach--diamond format)
	28 Jan. 1971	285	296	12c	Hawksbill turtle	Eretmochelys imbricata (Adult underwater--diamond format)
	"	286	297	20c	Turtle farm	(Small turtles in tanks--diamond format)
	10 Jan. 1972	297	309	2c	Underwater cable, turtle and telephone	(Green turtle by underwater cable)
	"	298	310	10c	"	"
	"	299	311	40c	"	"
	20 Nov. 1972	304	317	12c	Queen Elizabeth II, Prince Philip, hawksbill turtle and conch	(Small hawksbill)
	"	305	318	30c	"	"
	15 Jan. 1973	308	321	15c	$10 note and 10c coin	(Stylized turtle on coin)
	"	309a	MS323	15c	" (in SS)	"
	1974-75	335	350	6c	Blackbeard on Grand Cayman and green turtle	(Blackbeard with his foot on a green turtle)
	"	344	358	$1	Coat of Arms (w/w 314)	(Stylized turtle)
	19 Oct. 1977	344a	418	$1	Coat of Arms (w/w 373)	"
	30 July 1980		450	$1		" (but smaller stamp)
	15 Aug. 1979	428	491	20c	Rowland Hill and Cayman Islands No. 149	(Same as Scott 149)
	19 Dec. 1980	461	524	$2	Cayman Islands Arms	(Stylized turtle)
Chile	5 Sept. 1974	452a	730	200e	Easter Island turtle	Manutara Isla de Pascua (small stone turtle image--translation of "Manutara" is sooty tern)
Colombia	25 Apr. 1980	879a	1525	$4	"Learn to write"	Tortuga (Partial view of a green turtle)
Comoro Islands	20 Dec. 1965	65	51	20fr	Turtle	Tortue a ecailles
Cuba	1967	Not listed	1533	20c		(Diver pursuing a green turtle)
Djibouti	14 Sept. 1977	467	714	70fr		Chelonia mydas (Hawksbill underwater)
Dominica	10 Mar. 1969	253	257	48c	Diver and turtle	(Diver holding a small turtle)
	6 Sept. 1970	297	303	6c	Giant green turtle	Chelonia mydas (Turtle underwater)
		300a	M5307	6c	" (in SS)	"
Dominican Republic	30 Aug. 1980	C317		45c		Carey/Eretmochelys imbricata

Ascension 170

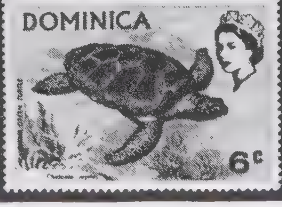
Bermuda 378

Cayman Is. 69

Cayman Is. 159

Country	Date issued	Catalog No.		Denomination	Description given in Scott	Wording on stamp and/or authors' brief description (in parentheses)
		Scott	Stanley Gibbons			
Fiji	3 Dec. 1962	164	299	1p	Queen Elizabeth II, turtles in bottom panels (w/w 4)	(2 small stylized turtles)
	14 Jan. 1964	176	311	1p	" (w/w 314)	"
French Polynesia	24 June 1976	289	219	18fr		Chelonia mydas (Stylized)
Gilbert Islands (Kiribati)	15 Jan. 1979	322	81	20c	Green turtle	Chelonia mydas caught by Cook's crew on Christmas Island for nourishment (Same as Dominica Scott 297)
Grenada	20 Jan. 1976	694	763	2c	Hawksbill turtle	Eretmochelys imbricata (Underwater)
Grenadines of St. Vincent	20 July 1978	Not listed	135	5c		Green turtle--Chelonia mydas
	"		136	40c		Hawksbill turtle--Eretmochelys imbricata
	"		137	50c		Leatherback turtle--Dermochelys coriacea
	"		138	$1.25		Loggerhead turtle--Caretta caretta
Guyana	15 Feb. 1978	268	686	15c	Giant sea turtle	Wildlife conservation (Green turtle underwater)
Indonesia	20 Dec. 1966	B206	1139	6r + 1r	Hawksbill turtle (incorrectly inscribed Chelonia mydas, green turtle)	Penju (Turtle underwater)
	17 Oct. 1979	1066	1561	150r	Leatherback turtle	Penyu belimbing--Dermochelys coriacea (Turtle underwater)
	17 Oct. 1979	1066a		200r	" (in SS)	"
Italy	3 Apr. 1978	1318	1547	170 l	Leatherback turtle	il mare deve vivere--Dermochelys coriacea
Jamaica	25 Feb. 1980	487	496	50c	Hawksbill and green turtles	(Stuffed specimens)
Japan	28 Jan. 1975	1204	1378	20y	Taro Urashima releasing turtle	(Folklore fisherman releasing turtle)
Jugoslavia	24 May 1980	1474	1878	3.40d	Loggerhead turtle	Caretta caretta (Incorrect number of scutes)
Kenya	27 June 1980	174	390	5sh	Hawksbill turtle	Marine life--Eretmochelys imbricata
Malaysia	31 Jan. 1972	95a	95	30c	Southeast Asian tourist attractions	(Small stylized leatherback with eggs)

Cuba SG-1533



Dominica 297

Indonesia B206

Italy 1318

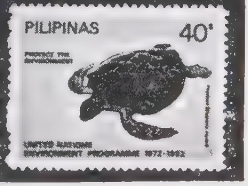
Country	Date issued	Catalog No.		Denomination	Description given in Scott	Wording on stamp and/or authors' brief description (in parentheses)
		Scott	Stanley Gibbons			
	4 Jan. 1979	179	194	$1	Leatherback turtle	Dermochelys coriacae [sic] (Adult on a beach)
Maldive Islands	17 Feb. 1980	841	852	1 1	Leatherback turtle	Dermochelys coriacea (Whole fish in mouth)
	"	842	853	2 1	Flatback turtle	Chelonia depressa (Male on a beach--incorrect number of scutes)
	"	843	854	5 1	Hawksbill turtle	Eretmochelys imbricata (Adult on a gravel beach)
	"	844	855	10 1	Loggerhead turtle	Caretta caretta young (Hatchling underwater)
	"	845	856	75 1	Olive ridley	Lepidochelys olivacea (Adult on a beach--incorrect number of scutes)
	"	846	857	10r	Atlantic ridley	Lepidochelys kempii (Turtle underwater--incorrect number of scutes)
	"	847		4r	Green turtle (in SS)	Save the turtles (Turtle crawling down a beach) *Chelonia mydas*
	29 Dec. 1980	897		90 1	Ridley turtle	(Hawksbill underwater)
Malta	10 Oct. 1979	564	631	5c	Loggerhead turtle	Caretta caretta (Turtle underwater)
Mauritania	1982			1 um		Tortue de luth--Dermochelys coriacer [sic]
	"			3 um		Tortue verte--Chelonia mydas
	"			4 um		Tortue a ecaille-- Eretmochelys imbricata
Mexico	1982			1p 60		Fauna de Mexico--tortuga de carey *Eretmochelys imbricata*
Mozambique	3 Mar. 1981	735		5mt	Loggerhead turtle	Animais Protegidos--*Caretta caretta*
New Caledonia	20 May 1978	437	599	30fr	Stylized turtle and globe	Protection de la tortue
	1980	452	629	23fr	Map of Pine Tree Island, fishermen with nets	Ile des pins (Small stylized turtle)
New Hebrides (British)	11 Feb. 1974	185	186	70c	Green sea turtle	Green sea turtle
New Hebrides (French)	11 Feb. 1974	204	F201	70c	Green sea turtle	Tortue verte de mer (Same as Scott 185, but in French)
Nicaragua	1979	Not listed	2230	90c		Tortuga "loggerhead" (Turtle underwater--fish in mouth)
	"		2231	$2.00		Tortuga Correoso (Leatherback underwater)
	"		2232	$2.20		Tortuga "Ridley" (2 turtles underwater)
	"		2233	$10.00		Tortuga Pico Halcon (Hawksbill underwater)
	"			$5.00 and $15.00		(Leatherback and green turtle--in SS)
	1980			$5.00		(Green turtle--in SS)

Japan 1204

Jugoslavia 1474

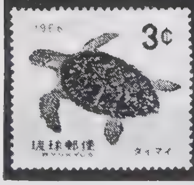
Maldive Is. 842

Maldive Is. 846

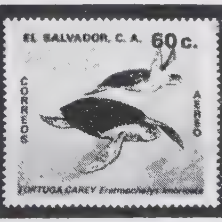


Philippines 1590

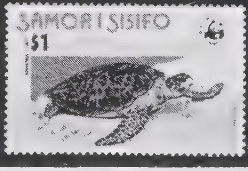
Country	Date issued	Catalog No.		Denomination	Description given in Scott	Wording on stamp and/or authors' brief description (in parentheses)
		Scott	Stanley Gibbons			
Pakistan	20 June 1981	547	560	40p	Green turtle	Green turtle Chelonia mydas (Turtle on a beach)
Philippines	5 June 1982	1590		40c	Turtle	Protect the environment--Pawikan Chelonia mydas, United Nations Environment Programme 1972-82
Pitcairn Is.	29 Sept. 1980	194	207	9c	Wooden turtles	(2 carved turtles)
Redonda (dependency of Antigua)	1980	Not listed		50c	Green turtle	Chelonia mydas (Turtle underwater)
Ryukyu Islands	20 Jan. 1966	137	172	3c	Hawksbill turtle	
El Salvador	1981		1665	60c		Tortuga Carey Eretmochelys imbricata (2 swimming hawksbills)
Samoa (Western Samoa)	18 June 1973	378A	399A	$2	Green turtle	Chelonia mydas (Adult on a beach)
	14 Apr. 1978	471	507	$1	Hawksbill turtle and Wildlife Fund emblem	Eretmochelys imbricata--World Wildlife Fund (Adult on a beach--Scott 470 shows hatchery but no turtles)
Sarawak	1 Oct. 1957	204	195	15c	Turtles (w/w 4)	(2 stylized turtles)
	17 Aug. 1965	220	209	15c	Turtles (w/w314)	"
Senegal	31 Jan. 1981	543	731	85fr	Turtle and crab, Madeleine Island	Tortue marine (Small stylized turtle)
		545c	MS733	85fr	" (in SS)	"
Seychelles	6 Feb. 1978	389	405A	10c	Hawksbill turtle	Tortue caret (Turtle underwater)
	14 Mar. 1980		405B	10c	"	(Same as Scott 389, but with 1979 at foot)
	16 Oct. 1978	420	436	5r	Green turtle	Tortue de mer--World Wildlife (Turtle underwater--incorrect scutes)
Seychelles Outer Islands (Zil Eloigne Sesel)	1980		Z	10c	Hawksbill turtle	(Same as Seychelles Scott 389)
Solomon Islands	5 Nov. 1958	105	96	L1	Coat of Arms	Stylized turtle in Coat of Arms
	15 June 1970	208	195	18c	British Solomon Islands Coat of Arms	"
	16 Dec. 1974	276	262	4c	Solomon Islands No. 208	" New Constitution 1974
	"	279	265	35c	"	" "
	"	279a	MS266	4c, 35c	" (in SS)	" "
	7 July 1978	372	363	45c	Coat of Arms	"
	16 Aug. 1979	395	386	35c	Rowland Hill and Solomon Islands No. 372	"
	20 Sept. 1982			$10		Hawksbill turtle, Eretmochelys imbricata



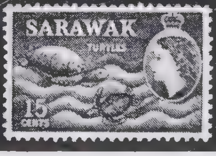
Ryukyu Is. 137



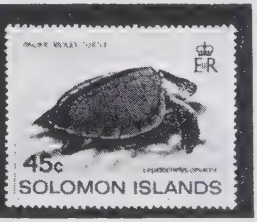
El Salvador SG-1665



Western Samoa 471

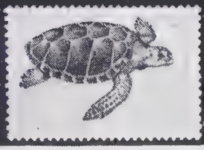


Sarawak 204



Solomon Is. New

Country	Date issued	Catalog No.		Denomination	Description given in Scott	Wording on stamp and/or authors' brief description (in parentheses)
		Scott	Stanley Gibbons			
	5 Jan. 1983			18c		Leatherback turtle, Dermochelys coriacea
	"			35c		Loggerhead turtle, Caretta caretta
	"			45c		Pacific ridley turtle, Lepidochelys olivacea
	"			50c		Green turtle, Chelonia mydas
Spanish Guinea	23 Nov. 1954	335	393	15c	Swimming turtle	(Green turtle underwater)
		B31	391	5c + 5c	"	"
Surinam	1982	591		5c	Caretta caretta	caretta caretta
	"	592		10c	Chelonia mydas	chelonia mydas
	"	593		20c	Dermochelys coriacae	dermochelys coriacae
	"	594		25c	Eretmochelys imbricata	eretmochelys imbricata
	"	595		35c	Lepidochelys olivacea	lepidochelys olivacea
Tonga	15 Dec. 1978	446	692	25s	Green turtle	Preservation of endangered species (Turtle on a beach--incorrect number of scutes)
	"	C251	697	31s	"	"
	"	CO152	O186	1p 10s	"	"
Trinidad and Tobago	7 July 1981	346	586	55c	Marine preservation	Environmental preservation--Our seas must live (Small stylized turtle)
		347a	MS588	55c+	(in SS)	"
Turks and Caicos Islands	14 Dec. 1948	98	214	2sh	Victoria and George VI	(2 small stylized turtles similar to Cayman Scott 69-80)
		99	215	5sh	"	"
		100	216	10sh	"	"
	29 May 1979	381	535	20c	Green turtle	Endangered species (Turtle underwater--incorrect number of scutes)
	2 Nov. 1979	402	578	2c	Goofy riding turtle	(Disney character on stylized turtle)
Tuvalu	21 Apr. 1976	22	29	35c	$1-coin and green turtle	New coinage (Turtle on coin and turtle underwater)
	1 July 1976	23	30	1c	Map of Niulakita, leathery turtle (w/w373)	Leathery turtle
	Sept. 1977	58	58	1c	" (No wmk.)	"
Vietnam (North)	1965	Not listed	N434	40x		Eretmochelys imbricata (Stuffed specimen)
	1975	"	N831	12x		Rua mui khe Dermochelys coriacae (Not a leatherback--stylized carapace)
Virgin Islands	10 Feb. 1979	348	399	22c	Hawksbill turtle	Conservation (Turtle laying eggs)
	"	349a	MS401	22c	Hawksbill turtle (in SS)	"
Yemen (People's Republic of Southern Yemen)	2 Sept. 1972	120	121	15f	Turtle	(Stylized turtle underwater)


Surinam 591

Turks and Caicos 98

Virgin Is. 348

15
جمهورية اليمن الديمقراطية الشعبية
PEOPLE'S DEMOCRATIC REPUBLIC OF YEMEN
Yemen 120

Addendum.—Issues that are in need of verification, and issues in which marine turtles only appear in the border of sheets and not on the stamp itself.

Country	Date issued	Catalog No.		Denomination	Description given in Scott	Wording on stamp and/or authors' brief description (in parentheses)
		Scott	Stanley Gibbons			
Antigua and Barbuda	1982			$5		(SS of flora and fauna commemorating centenary of Charles Darwin's death--turtle in the bottom right border)
Cayman Islands	29 May 1979	372		10c	American Bicentennial	(Turtle in border)
	"	373		15c	"	"
	"	374		20c	"	"
	"	375		25c	"	"
	"	376		30c	"	"
	"	376a			"	" (in SS)
Grenadines of Grenada		Not listed		2c	Hawksbill turtle	(Listed by Riemer and Allen 1983 as an overprint of Grenada Scott 694--not verified)
Nicaragua		Not listed		90c $2.00 $2.20 $10.00		(Listed by Riemer and Allen 1983 as the same as Nicaragua Stanley Gibbons 2230-2233, but without 5 red Olympic circles--not verified)

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Edgardo D. Gomez
Marine Sciences Center
University of the Philippines
Diliman, Quezon City 3004
Philippines

and

George H. Balazs
National Marine Fisheries Service
Southwest Fisheries Center Honolulu Laboratory
P.O. Box 3830
Honolulu, Hawaii 96812
U.S.A.

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Evolution, 37(1), 1983, pp. 30–37

KINETIC AND ELECTROPHORETIC DIFFERENTIATION OF LACTATE DEHYDROGENASES OF TELEOST SPECIES-PAIRS FROM THE ATLANTIC AND PACIFIC COASTS OF PANAMA

John E. Graves[1], Richard H. Rosenblatt, and George N. Somero
Marine Biology Research Divison (A-002), Scripps Institution of Oceanography,
University of California, San Diego, La Jolla, California 92093

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The important role of molecular adaptations in evolution has been demonstrated in studies of enzymic and respiratory proteins of organisms living in different habitats. Investigations of homologous proteins of warm- and cold-adapted ectotherms, for example, have elucidated many of the critical molecular properties that are involved in adaptation to different environments (Somero, 1978). However, even though substantial information is available on adaptive differences among homologous proteins of widely different species, e.g., those belonging to different families and genera, there remains much to be learned of the role of fine-scale adaptations, as might be important in populations of a single species that inhabit slightly different environments.

Substantial amounts of protein variation, both between populations of a single species and between closely related species, have been demonstrated with electrophoretic techniques (reviewed in Powell, 1975), and the existence of allelic variants which cannot be distinguished by standard electrophoretic methods has also been reported in comparisons of populations and species (Bernstein et al., 1973; Johnson, 1975; Siebenaller and Somero, 1978). The role of these electrophoretically detectable and cryptic allelic variants in molecular evolution has become an important focus of contemporary evolutionary study (Lewontin, 1974). Is the observed allelic variation of functional significance in many cases? Or is this variation generally lacking in selective importance? A closely related question, and one serving as a major focus of the present study, is what degree of environmental variation is required to select for functionally different proteins?

One approach to addressing these questions experimentally is to study a given class of enzyme in several populations of closely related organisms that are separated by a common faunal barrier into habitats that differ in an environmental factor such as temperature. Comparisons of protein homologues of these populations may provide especially good insight into the role of fine-scale molecular adaptation. However, in order for such a comparison to be meaningful, several conditions must be met. First, one must know in advance, from broadly comparative studies of the protein in question, what values are to be expected for the functional trait(s) under investigation. Only with this strong empirical base can the observed allelic variations be interpreted. Second, the populations studied must have existed in the different habitats for long enough periods of time for the accumulation of new protein variants. Third, functional analysis of the allelic variants must be performed under *in vitro* conditions which simulate, as closely as possible, the *in vivo* conditions to which the proteins are normally exposed.

An excellent opportunity for an investigation which meets these criteria is provided by the Panama land bridge, which arose approximately 3.1 million years ago (Keigwin, 1978), isolating a presumably very similar fauna of tropical marine shore fishes in significantly different thermal environments. During the dry season (December to May), strong offshore winds cause the upwelling of cold, nutrient-rich waters in the Pacific. Water temperatures in the Gulf of Panama have been recorded to drop by as much as 15 C in 48 hours (Hildebrand, 1939). The upwelling events are unpredictable, and rapid cooling is often followed by a gradual rise in surface temperatures. Not all areas of the eastern tropical Pacific experience intense upwellings, and there is much annual and geographical variability in both the duration and intensity of the upwelling events (Schaeffer et al., 1958). The Atlantic waters do not undergo these changes, and have a mean temperature 2–3 C higher than the Pacific waters, as well as a much smaller temperature range. The differences in thermal regime on the two coasts of Panama have favored selection for altered thermal tolerances between Atlantic and Pacific species. Graham (1971) found that the Pacific members of species pairs (congeners having close relatives on either side of the Isthmus) have lower lethal temperatures than their Atlantic congeners, when acclimated to the same temperature.

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[1] Current address: Southwest Fisheries Center, NMFS, P.O. Box 271, La Jolla, California 92038.

In this study we have examined four species pairs to determine if adaptation at the enzyme level has also been favored by the different thermal regimes of the Atlantic and Pacific coastal waters. A considerable amount of electrophoretically detectable protein variation has been found between congeneric fishes from these two habitats (Vawter et al., 1980), suggesting the possibility of functional differentiation between the proteins of the species pairs. That the slight temperature differences between these two habitats may be sufficient to lead to adaptive differences in enzyme function is suggested by the fact that, of the few studies which have demonstrated functional allelic differences between closely related populations and species, most have involved kinetic differences with respect to temperature (Koehn, 1969; Merritt, 1972; Vigue and Johnson, 1973; Day et al., 1974; Place and Powers, 1979; Graves and Somero, 1982). For example, comparisons of allelic variants of lactate dehydrogenases in congeners of the barracudas (genus *Sphyraena*) showed that temperature differences of only 5–8 C are sufficient to select for temperature-adaptive differences in this enzyme (Graves and Somero, 1982).

The present study examines variants of skeletal muscle type (M_4 or A_4) lactate dehydrogenase (LDH. E.C. 1.1.1.27; lactate : NAD oxidoreductase) due to the wealth of kinetic information available for interspecific homologues of this protein and its critical role in locomotory function of fishes (Somero and Childress, 1980). Fully purified M_4-LDHs from four species pairs are characterized in terms of apparent Michaelis constants (K_m) of pyruvate and catalytic rate constants (k_{cat}), using physiologically realistic temperature and pH values. In two of the four species pairs, K_m and k_{cat} values displayed temperature-adaptive patterns between congeners comparable to those found in other studies of the enzyme. In the two other cases, the LDHs of the congeners were kinetically indistinguishable. There was no correlation between kinetic differences and electrophoretic differentiation.

MATERIALS AND METHODS

The four species pairs chosen for this study ([Atlantic and Pacific species of each pair, respectively] damselfishes: *Abudefduf taurus* and *A. concolor*; groupers: *Epinephelus cruentatus* and *E. panamensis*; blennies: *Ophioblennius atlanticus* and *O. steindachneri*; and wrasses: *Thalassoma bifasciatum* and *T. lucasanum*) are common on both coasts of Panama. Members of a pair are ecologically and morphologically extremely similar (Meek and Hildebrand, 1927), and they occupy the same types of habitat, occur over the same depth ranges, and have similar diets. The major physical difference between the environments of the pairs is temperature.

Specimens were collected on trolled lures, with pole spears, and with quinaldine and hand nets on the two coasts of Panama. Collections were made during March 1979 and March 1980 (Panama Atlantic water temperature of 26–28 C; Panama Pacific water temperature of 15–19

C) and during September 1977 (Panama Atlantic water temperature of 27–30 C; Panama Pacific water temperature of 27–30 C). The fish were immediately frozen and shipped to the laboratory at Scripps on dry ice, where they were stored until use at −35 C.

Purification of the M_4-isozyme of LDH followed the procedures of Graves and Somero (1982), with the exception that the fractions containing the highest LDH activity from the affinity chromatography step were not concentrated by ultrafiltration, but were pooled and stored at 5 C. Loss of enzymic activity of the pooled peak fractions over the three days required to perform the kinetic studies was less than 5%. Enzyme purity was determined in each case by sodium dodecyl sulfate polyacrylamide gel electrophoresis (Laemmli, 1970). M_4-LDH was purified from two individuals of each *Abudefduf* and *Epinephelus* species. Because of their small sizes, several individuals of each *Ophioblennius* and *Thalassoma* species were pooled for purification after they were electrophoretically phenotyped. Kinetic differences were not detected between Pacific fishes collected in March (cold temperatures) and September (warm temperatures).

Two parameters of enzyme function were determined from the fully purified enzyme preparations. The apparent (=graphically determined) Michaelis constant (K_m), which for this reaction provides an approximation of enzyme-substrate affinity, was determined at 10 C, 20 C, and 30 C. The catalytic constant (k_{cat}), which is a measure of maximal catalytic efficiency (the maximal reaction velocity that a molecule of the enzyme can generate) was determined at 20 C. Both K_m and k_{cat} values were determined using a weighted linear regression analysis of Lineweaver-Burk plots (Wilkinson, 1961). Eight concentrations of pyruvate (0.2 to 1.0 mM) were used for each K_m and k_{cat} determination.

Horizontal starch gel electrophoresis of the purified M_4-LDHs was performed after the kinetic studies to determine within species variability of M_4-LDH and to determine whether a correlation existed between kinetic differentiation and electrophoretic variation. 12.5% (weight : volume) starch gels (Electrostarch lot #307) were run in tris-citrate buffer, pH 8.0, and Poulik buffer, pH 8.7, for 6 h at 60 mA (Selander et al., 1971). At least 10 individuals of each species were electrophoretically surveyed, and no within species variability of M_4-LDH phenotype was noted in any of the eight species.

RESULTS AND DISCUSSION

Functional allelic differences were discovered between the M_4-LDHs of two of the species pairs. The kinetic data (Table 1) show that differences in both the apparent K_m of pyruvate and k_{cat} exist between the Pacific and Atlantic species of *Thalassoma* and *Ophioblennius*. In both pairs the enzyme of the Pacific species appears to be "cold-adapted" relative to the enzyme of the Atlantic congener. Thus, in agreement with studies of widely different vertebrates (fishes, reptiles and mammals) having extremes of body temperature between −2 C (Antarctic fishes) and 47 C (desert reptile), the LDHs of these two Pacific species have inherently higher K_m of pyruvate values at any given temperature than the LDHs of the more warm-adapted Atlantic congeners. These temperature-related differences in K_m favor a marked stabilization of K_m at physiological temperatures, as shown by the summary of existing data given in Figure 1. This high degree of conservation of K_m in different species at their appropriate body temperatures has been interpreted as an adaptation insuring that enzymes retain a reserve capacity for increasing rate of catalysis as substrate concentrations rise during metabolic activations, e.g., during bursts of locomotion. Thus, by stabilizing K_m values in a range that is close to, or somewhat greater than, physiological substrate concentrations, an enzyme is able to attain a significant fraction of its potential velocity ($V_{\max}$) under normal physiological conditions and also increase its activity as substrate levels rise (Fersht, 1977; Graves and Somero, 1982). It bears noting that

TABLE 1. *Kinetic parameters of M_4-LDHs purified from closely related species separated by the Isthmus of Panama.* K_m *of pyruvate values were determined from Lineweaver-Burk plots of reaction velocity versus pyruvate concentration (eight different [pyruvate] were used in each case), using the weighted linear regression method of Wilkinson (1961). The* k_{cat} *values are based on theoretical maximum reaction velocities, which also were computed by the weighted linear regression method of Wilkinson (1961).*

Species	K_m of pyruvate (mM) ± 95% CI			k_{cat} (sec^{-1}) ± 95% CI
	10 C	20 C	30 C	20 C
Abudefduf taurus (Atlantic)	0.121 ± 0.007	0.172 ± 0.022	0.309 ± 0.030	357 ± 10
Abudefduf concolor (Pacific)	0.123 ± 0.009	0.154 ± 0.018	0.298 ± 0.024	332 ± 8
Epinephelus cruentatus (Atlantic)	0.073 ± 0.007	0.121 ± 0.006	0.212 ± 0.023	243 ± 3
Epinephelus panamensis (Pacific)	0.086 ± 0.012	0.125 ± 0.013	0.208 ± 0.011	294 ± 6
Ophioblennius atlanticus (Atlantic)	0.121 ± 0.007	0.188 ± 0.018	0.292 ± 0.013	173 ± 5
Ophioblennius steindachneri (Pacific)	0.189 ± 0.017	0.237 ± 0.022	0.396 ± 0.033	280 ± 9
Thalassoma bifasciatum (Atlantic)	0.072 ± 0.008	0.115 ± 0.012	0.248 ± 0.027	125 ± 2
Thalassoma lucasanum (Pacific)	0.106 ± 0.010	0.142 ± 0.012	0.298 ± 0.027	370 ± 8

this strong conservation of K_m of pyruvate is seen only when the *in vitro* assay medium has the appropriate pH for the temperature of measurement (Yancey and Somero, 1978; Somero, 1981). Thus, the detection of functionally significant differences between enzyme variants may be contingent on the use of physiologically realistic assay conditions, especially pH and temperature (cf. Place and Powers, 1979).

The differences in k_{cat} between the M_4-LDHs of the Atlantic and Pacific congeners of *Thalassoma* and *Ophioblennius* also are temperature compensatory. For both pairs of fishes, the Pacific species possesses the LDH variant with the higher catalytic rate potential. These k_{cat} data agree with findings made using widely different vertebrate species, which show that k_{cat} values for a variety of different enzymic reactions including the LDH reaction vary inversely with adaptation temperature (Low et al., 1973; Borgmann and Moon, 1975; Low and Somero, 1976; Johnston and Walesby, 1977; Somero, 1978; Somero and Siebenaller, 1979; Graves and Somero, 1982). Thus, the differences between the M_4-LDHs of the congeners of *Thalassoma* and *Ophioblennius* suggest that very small differences in body temperature are sufficient to favor selection for temperature adaptive differences in enzyme kinetic properties, a finding consistent with the comparisons of barracuda congeners having 5–8 C differences in average body temperature (Graves and Somero, 1982).

The lack of kinetic differences between the M_4-LDH homologues of the *Abudefduf* and *Epinephelus* species pairs cannot be explained in adaptive terms, and may simply reflect the lack of appropriate mutations (i.e., mutations of the types which we propose to have occurred in the other two species pairs) subsequent to the splitting of the original populations of these species.

The K_m of pyruvate values of the LDHs of the four species pairs all fall within the range of K_m values expected for vertebrate M_4-LDHs at normal body temperatures, 0.15 to 0.30 mM pyruvate (Fig. 1). How-

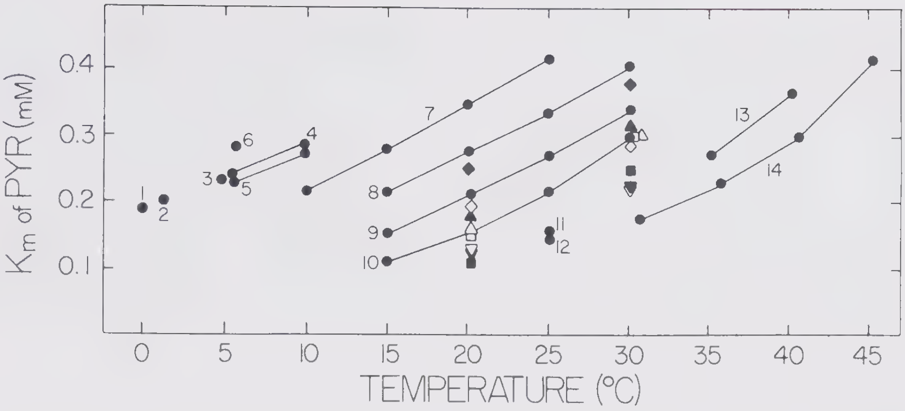

FIG. 1. Apparent K_m of pyruvate values for purified M_4-LDHs of selected vertebrate species having widely different body temperatures. Assays were performed using the physiologically realistic, temperature-dependent pH regime described by Yancey and Somero (1978). Assays were conducted at normal body temperatures of each species plus, in some cases, at temperatures outside the physiological range (see below). The species studied and their temperature ranges are 1. *Pagothenia borchgrevinki* (Antarctic nototheniid fish; −1.86 C), 2. *Halosauropsis macrochir* (deep-sea halosaur fish; 2–3 C), 3. *Coryphaenoides acrolepis* (Pacific rattail fish; 2–3 C), 4. *Sebastolobus alascanus* (shortspine thornyhead fish; 3–10 C), 5. *Hippoglossus stenolepis* (Pacific halibut fish; 4–12 C), 6. *Antimora rostrata* (deepsea flatnose codling fish; 2–6 C), 7. *Thunnus thynnus* (bluefin tuna fish; 5–30 C), 8. *Sphyraena argentea* (California barracuda fish; 14–22 C), 9. *Sphyraena lucasana* (Cortez barracuda fish; 16–28 C), 10. *Sphyraena ensis* (Panama barracuda fish; 22–30 C), 11. *Hypostomus plecostomus* (Amazon armoured catfish; 20–30 C), 12. *Potamotrygon* sp. (South American freshwater stingray fish; 25–30 C), 13. *Oryctolagus cuniculus* (New Zealand white rabbit; 37–39 C), and 14. *Dipsosaurus dorsalis* (desert iguana reptile; preferred temperatures of 36–42 C, and upper distribution limit at 47 C; Norris [1953]). K_m data are from Yancey and Somero (1978) (species 1, 5, 7, 11–13), Graves and Somero (1982) (species 8–10), Somero et al. (1982) (species 2–4, 6) and Donahue and Somero (unpubl.) (14). Symbols for this study: *Abudefduf taurus* (▲), *A. concolor* (△), *Epinephelus cruentatus* (▼), *E. panamensis* (▽), *Ophioblennius atlanticus* (◇), *O. steindachneri* (◆), *Thalassoma bifasciatum* (■), and *T. lucasanum* (□).

ever, within the 0.15 to 0.30 mM range, there is variation among species that appears related to taxonomic affinity. For example, both *Abudefduf* LDHs have K_m values that are statistically indistinguishable, but which are significantly lower at all temperatures than the K_m values of the *Epinephelus* species' LDHs, which also are statistically indistinguishable at all temperatures. The values for the K_m of the *Ophioblennius* species' LDHs at physiological temperatures are near 0.27 mM pyruvate, a value close to that found for the K_m of pyruvate for LDHs of four barracuda species (0.26 mM) at these species' normal physiological temperatures (Graves and Somero, 1982). For the *Thalassoma* species, however, the K_m of pyruvate is conserved near 0.21 mM. The significance of what appear to be slightly different "set points" for the K_m of pyruvate in different genera of fishes remains to be established.

Of the two species pairs that displayed functional differences in their M_4-LDHs, the *Thalassoma* species had alleles which were electrophoretically distinguishable, whereas the *Ophioblennius* species were electrophoretically indistinguishable (Fig. 2). In addition, of the two pairs which did not demonstrate functional allelic differences at the *M_4-Ldh* locus, one pair (*Epinephelus*) exhibited electrophoretic differences and the other (*Abudefduf*) did not. Thus, in the four species pairs examined, there was no correlation between electrophoretic and functional differentiation.

The lack of correlation between electrophoretic and functional differentiations of these species may be a consequence of the small number of species studied, but this lack of correlation does reflect on the possible outcomes of protein variation. Certain sections of protein amino acid sequences are well-conserved between homologous proteins and between proteins with similar functions, but which are coded by different gene loci (analogous proteins; see Dayhoff, 1972). X-ray diffraction studies have demonstrated several of these well-conserved sequences in active sites and in areas which are important for determining conformational folding (Buehner et al., 1973; Taylor et al., 1973; Rossmann et al., 1974). As suggested by King and Jukes (1969), non-conservative amino acid substitutions in these regions are likely to produce dramatic changes in protein function, while amino acid substitutions in other, less-conserved sequences may produce no detectable change in enzyme function. An example of the latter type has been reported for LDH (Eventoff et al., 1977). The number of histidyl residues (a residue which is approximately half-protonated at physiological pH) on the exterior of the enzyme varies greatly, both between species and between isozyme forms. However, the internal and active site histidyl residues are highly conserved. Thus, depending on the location of an amino acid substitution involving a charge change, functional differences may or may not result. The demonstration of electrophoretically cryptic kinetic differentiation in LDHs (this study; Siebenaller and Somero, 1978) and the occurrence of electrophoretic differentiation in kinetically indistinguishable LDHs (this study) may reflect variations in charged amino acid residues, e.g., histidyls, at both conserved and non-conserved sites. Furthermore, kinetic differences may be due to amino acid substitutions causing no net charge alteration. The kinetic differences between the heart- and muscle types of LDHs of vertebrates are due largely to an alanyl to glutaminyl substitution in the cofactor binding domain, a substitution which conserves net charge (Eventoff et al., 1977).

One objective of this study was to determine the fraction of functionally significant allelic variation between two closely related species at a single gene locus. Two of the four species pairs displayed significant kinetic differences in their M_4-LDHs and, in both cases, the Pacific species was more "cold-adapted." These data are of course insufficient to allow predictions about the abundance of functional allelic variation in other instances, as the amount of kinetic variation detected between proteins of other species may be dependent on the protein investigated, the magnitude and constancy of the environmental differences between the species, and the length and nature of the barriers to gene flow between groups. However, the results of this study, and others in which closely related species from different environments have been investigated, clearly demonstrate that substantial functional allelic variation exists within and between natural populations.

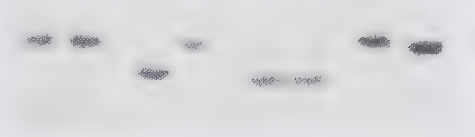

FIG. 2. Electrophoretic mobilities of M_4-LDHs of closely related fish species separated by the Isthmus of Panama. From left to right: *Abudefduf taurus, A. concolor, Epinephelus cruentatus, E. panamensis, Ophioblennius atlanticus, O. steindachneri, Thalassoma bifasciatum,* and *T. lucasanum.*

The use of enzyme kinetics to investigate functional allelic variation has advantages over other approaches which have been used, e.g., intensity of gel staining and thermal stability. Of key importance is that kinetic measurements, when obtained in physiologically appropriate media, reflect enzyme performance under typical cellular conditions. Thus, kinetic differences detected *in vitro* could reflect true differences in metabolic flux and power output during times of thermal stress to the organism.

It is not known how large an environmental, e.g., thermal, difference needs to be before it becomes selective for molecular fine-tuning. Previous work with congeneric barracudas demonstrated that mean environmental (body) temperature differences of only 5–8 C were sufficient to promote molecular adaptation. In this study a mean environmental temperature difference of 2–3 C and, possibly of more importance, a much cooler temperature range in the Pacific, appears to have provided a selective force favoring fine-scale molecular adaptation. It is also important to note that these adaptations have occurred even though the Pacific fishes do not experience upwelling (cooling) events over their entire ranges. Thus, in the absence of gene flow, very small changes in the physical environment may be sufficient to promote enzymic adaptations.

SUMMARY

Many populations of marine shore fishes were separated by the uplift of the Isthmus of Panama approximately three million years ago. Since the time of separation, the populations have been exposed to different thermal environments. Due to strong, but geographically and temporally variable, upwelling events, the Pacific fishes experience a more variable temperature regime and a cooler mean temperature than their Atlantic congeners. Kinetic analysis of muscle-type lactate dehydrogenases, purified from white skeletal muscle of four species pairs, revealed significant functional differences in both apparent Michaelis constants of pyruvate and catalytic rate constants between members of two of the four pairs. In both cases the Pacific species were more cold-adapted than their Atlantic congeners, demonstrating that in the absence of gene flow, small environmental differences can lead to molecular adaptation. Horizontal starch gel electrophoresis of the purified enzymes revealed distinct allelic forms between members of two of the four pairs. However, the electrophoretic differences were not correlated with the functional differences. This lack of correlation is consistent with the hypothesis that the nature and location of an amino acid substitution determines whether the allele is selectively significant or neutral.

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Department of Fisheries and Wildlife Sciences,
Virginia Polytechnic Institute and State University,
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HAWAIIAN SEABIRD FEEDING ECOLOGY

by

CRAIG S. HARRISON, THOMAS S. HIDA, AND MICHAEL P. SEKI

OCTOBER 1983 NO. 85

FRONTISPIECE. White tern carrying flyingfish (*Parexocoetus brachypterus*), French Frigate Shoals.

HAWAIIAN SEABIRD FEEDING ECOLOGY

CRAIG S. HARRISON[1]
U.S. Fish and Wildlife Service, P.O. Box 50167, Honolulu, HI 96850

THOMAS S. HIDA
Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 3830, Honolulu, HI 96812

MICHAEL P. SEKI
Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 3830, Honolulu, HI 96812

Abstract: The Northwestern Hawaiian Islands are the nesting grounds of about 10 million seabirds of 18 species. Fishery development proposals for this area led to a need for food habit studies of these birds to aid in their management. Food habits are diverse, with 56 families of fish, 8 families of squid, and 11 groups of crustaceans identified. Similar to other tropical seabird communities, this community feeds largely on flyingfishes and squids. In addition, however, this community consumes many *Decapterus* spp., juvenile goatfishes, juvenile lizardfishes, and mesopelagic fishes that rarely occur in the diets of tropical seabirds elsewhere. Albatrosses fed largely on squids and flyingfish eggs. They also ate many mysids, isopods, leptostracans, and shrimps that occur in very deep water. Pelecaniforms ate large flyingfishes and *Decapterus* spp., many of which were more than 25 cm in length. Squids, especially the surface-dwelling Ommastrephidae, were consumed frequently. Certain boobies ate Pacific sauries, anchovies, and juvenile goatfishes at some locations. The terns and shearwaters that usually feed in association with predatory fishes ate 2–8 cm prey, especially small ommastrephid squids and juvenile forms of flyingfishes, goatfishes, lizardfishes, and *Decapterus* spp. Small nocturnal-feeding procellariiforms ate many 1–3 cm mesopelagic organisms such as lanternfishes, hatchetfishes, bristlemouths, and squids. Small terns ate primarily juvenile flyingfishes, goatfishes, lizardfishes, dolphin-fishes, and a cow fish. In addition, the blue-gray noddy ate minute prey such as seastriders and copepeds. Most birds feed most of their young during the spring and summer. Breeding in the Northwestern Hawaiian Islands is correlated with and may be controlled by the period of maximum availability of food. Breeding seasons for seabirds in tropical climates are generally less predictable compared to seabird communities in temperate or cold water regimes. The relative predictability of the breeding season for tropical seabirds in the Hawaiian Archipelago may be explained by the fact that most islands there are subtropical. Many seabirds in Hawaii breed at the northern extent of their range. Some seabird species breed largely during winter. Several of these species are adapted for nocturnal feeding. Other winter breeding species may be outcompeted for nesting sites during spring and summer by larger species that have similar nesting requirements. Poor weather conditions during winter may also encourage spring and summer breeding for some species. All seabirds were opportunistic and fed on a wide variety of shoaling fish and squid. They apparently took any organism of appropriate size that occurred in surface waters. Variation in diet for most species was more correlated with season than with location. Some resource partitioning among species was evident both in the composition and in the size of prey. Differences in diet may reflect differences among species in morphology, feeding technique, time of day that feeding occurs, seasonality of breeding, or feeding location. The most numerous species in this community are those that ate many squid. The population differences among species may be merely another expression of the proposition that pelagic feeding seabirds are more numerous than inshore feeding seabirds in tropical waters. Many fundamental questions concerning the biology of tropical and subtropical seabirds cannot be answered until better methods of measuring the availability of prey are developed. Our results will enable wildlife and fishery managers to more accurately predict the effects of various fisheries on marine birds

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[1] Present address: Environment and Policy Center, The East-west Center, 1777 East-west Road, Honolulu, HI 96848

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INTRODUCTION

No comprehensive work has been published on the diets of Hawaiian seabirds, and most of the information that does exist is fragmentary or anecdotal (e.g., Munro 1944, Berger 1972). Brown (1975) gave quantitative information on the diets of sooty terns and brown noddies breeding on Manana Island (Oahu), and Ashmole and Ashmole (1967*a*) presented limited information on the diet of the red-footed booby on Oahu (scientific names of birds are given in Appendix 1). Feeding habits of several species may be inferred from studies on Christmas Island (Pacific Ocean) by Ashmole and Ashmole (1967*b*) and Schreiber and Hensley (1976). Christmas Island is 2,000–3,000 km south of the Hawaiian Archipelago.

Fishery development proposals for spiny lobsters, carangids, snappers, and live bait for tuna fishing in the Northwestern Hawaiian Islands (NWHI) prompted the U.S. Fish and Wildlife Service and the National Marine Fisheries Service to investigate ecological relationships that could be altered by intensive harvest of various target species. Altered food webs could potentially affect seabirds, which are abundant in this area. The NWHI are the nesting grounds of an estimated 10 million seabirds of 18 species (Table 1). Many of their breeding islands have been protected since 1911. Because seabird population crashes were correlated with fishery development in Peru (Schaefer 1970, Idyll 1973), Southwest Africa (Crawford and Shelton 1978), and California (Ainley and Lewis 1974) it seemed imperative that the feeding ecology of Hawaiian seabirds be documented before fishery development Few integrated studies of the diets of large, complex seabird communities have been published. The work on 18 species in the Barents Sea (Belopol'skii 1957), 11 species on Christmas Island (Ashmole and Ashmole 1967*b*, Schreiber and Hensley 1976), and 9 species in the North Sea (Pearson 1968) elucidated the interspecific feeding relationships of colonial nesting birds in those parts of the world. The present study was designed to provide an understanding of the trophic structure of the unique seabird community in the subtropical NWHI. Results should be useful to both community ecologists and resource managers. When feasible, ancillary food samples were collected in the main Hawaiian Islands. A preliminary report of this work has been published elsewhere (Harrison and Hida 1980).

Table 1. Maximum recent population estimate (individual birds), Northwestern Hawaiian Islands.[a]

	Nihoa	Necker	French Frigate Shoals	Gardner Pinnacles	Laysan	Lisianski	Pearl and Hermes Reef	Midway	Kure
Black-footed albatross	100	350	4,700	0	67,000	3,500	14,000	30,000	600
Laysan albatross	tr[b]	1,800	1,600	tr	550,000	8,000	45,000	500,000	2,400
Bonin petrel	0	0	750	0	40,000	1,000,000	1,000	10,000	2,500
Bulwer's petrel	250,000	200	500	tr	20,000	tr	tr	0	0
Wedge-tailed shearwater	25,000	4,500	13,000	tr	1,000,000	500,000	26,500	20,000	1,500
Christmas shearwater	800	0	tr	0	10,000	2,000	tr	100	tr
Sooty storm-petrel	tr	0	tr	0	2,500	0	7,500	0	0
Red-tailed tropicbird	500	200	450	100	4,000	4,500	200	3,000	2,000
Masked booby	350	500	1,200	800	2,000	1,200	600	20	100
Red-footed booby	3,500	1,400	750	tr	2,500	3,000	200	1,000	600
Brown booby	225	50	135	20	250	200	200	tr	100
Great frigatebird	10,000	2,000	1,400	250	8,000	2,500	900	200	500
Sooty tern	100,000	50,000	250,000	750	2,000,000	1,700,000	80,000	50,000	12,000
Gray-backed tern	10,000	7,500	1,750	4,000	40,000	15,000	1,900	50	100
Blue-gray noddy	2,500	2,500	tr	tr	0	0	0	0	0
Brown noddy	20,000	50,000	10,000	5,000	30,000	15,000	8,400	3,000	1,200
Black noddy	2,000	1,000	11,000	400	5,000	5,000	4,300	5,000	2,000
White tern	3,000	600	3,700	400	1,500	500	tr	6,000	tr

[a] Data from Amerson (1971), Clapp (1972), Woodward (1972), Ely and Clapp (1973), Amerson et al. (1974), Clapp and Wirtz (1975), Clapp et al. (1977), and Clapp and Kridler (1977). Estimates from Midway are our own

[b] tr Indicates species is present in low but undetermined numbers

The species studied were the black-footed albatross, Laysan albatross, Bonin petrel, Bulwer's petrel, wedge-tailed shearwater, Christmas shearwater, sooty storm-petrel, red-tailed tropicbird, masked booby, red-footed booby, brown booby, great frigatebird, sooty tern, gray-backed tern, blue-gray noddy, brown noddy, black noddy, and white tern. Both albatrosses nest primarily in the NWHI (Palmer 1962). Bonin petrels and sooty storm-petrels breed in the Volcano Islands in addition to islands in the study area (King 1967). Christmas shearwaters, gray-backed terns, and blue-gray noddies breed at various locations in the tropical Pacific (King 1967). Bulwer's petrels nest on islands in the warmer waters of the Atlantic and Pacific but not the Indian Ocean (Alexander 1954). Red-tailed tropicbirds (Fleet 1974) and wedge-tailed shearwaters (Alexander 1954) nest in the tropical Indo-Pacific but not the Atlantic Ocean. The boobies (Nelson 1978), great frigatebird (Nelson 1975), sooty tern, white tern, brown noddy, and black noddy (Alexander 1954) are widespread pantropic species.

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History, supplied reprints, identifications, and referrals; Lanna Cheng, Scripps Institution of Oceanography, identified *Halobates* species; Walter Matsumoto, National Marine Fisheries Service, Honolulu Laboratory, aided in the identification of larval and juvenile scombrids; John E. Fitch (deceased), California Department of Fish and Game, identified several myctophid otoliths; Frederick H. Berry, National Marine Fisheries Service, Miami Laboratory, helped identify *Seriola* spp.; Tadashi Kubota, Tokai University, furnished *Decapterus* specimens; A. Binion Amerson, Jr., identified ticks; the captain and crew of the research vessel *Townsend Cromwell* provided logistic support of field personnel during the sampling program; Sally H. Kuba wrote the computer programs used in this study; Bernie M. Ito photographed the fishes; Tamotsu Nakata drew figures.

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THE NORTHWESTERN HAWAIIAN ISLANDS

The biologically isolated Hawaiian Archipelago is 4,000 km from the nearest continental land mass and stretches about 2,600 km from Hawaii to Kure Atoll (Fig. 1). Each small island between Nihoa and Kure is associated with a relatively large bank. Nihoa and Necker are remnant volcanic cones of 63 and 17 ha, respectively (Clapp et al. 1977, Clapp and Kridler 1977). French Frigate Shoals is a coral atoll consisting of 12 sandy islets and 1 volcanic pinnacle on a 360-km^2, crescent-shaped lagoon with a total land area of 45 ha (Amerson 1971). Gardner Pinnacles are 2 small volcanic rocks of approximately 1.2 ha (Clapp 1972). Laysan, 20% of which is an interior brackish lagoon (Ely and Clapp 1973), is a coral island of about 370 ha atop a massive submerged volcanic peak. Lisianski is a low sandy coral island of 182 ha at the northern end of a 170-km^2 bank (Clapp and Wirtz 1975). Pearl and Hermes Reef is an atoll comprised of 9 low, coral islands, 4 of which are nonvegetated sand bars. The land mass of 34 ha is scattered in a 370-km^2 lagoon (Amerson et al. 1974). Midway is a coral atoll consisting of 2 islands with a total land area of 550 ha, the largest in the NWHI (Gross et al. 1969). Kure is the northernmost coral atoll in the world, and consists of 2 islands with a land area of about 100 ha and a lagoon with an area of 46 km^2 (Gross et al. 1969, Woodward 1972). A more complete description of each island may be obtained by consulting the references cited above.

Northeastern trade winds predominate throughout most of the year. Surface water temperatures range from 20–25 C from

November–February and from 25–27.5 C from April–August (Fig. 1). The Hawaiian Islands are bathed by central North Pacific water that is seasonally displaced by the California current extension in spring and summer (Seckel 1962). Storms and associated high winds and swells are frequent from November–March.

METHODS

During the course of this study, we measured several morphological characters of each seabird species, including weight, bill width, and culmen length. Observations of breeding stage of each species by field personnel were recorded to determine the breeding chronologies of each species.

Field Collection of Food Samples

The 4,315 food samples that provide the basis for this paper were collected from 1978–81 on an irregular series of visits to various islands in the study area. Cruises in August–September 1978, May 1979, and June 1980 allowed visits to all islands between Nihoa and Kure (Fig. 1). Cruises in February–March 1978 included Laysan and Midway; May 1978 included French Frigate Shoals, Laysan, and Lisianski; July 1978 included French Frigate Shoals, Laysan, Lisianski, Pearl and Hermes Reef, and Midway; November 1980 included all islands except Lisianski and Kure; January–February 1981 included Laysan and Nihoa. Visits to Midway occurred during the following months: October and November 1978; January, February, August, September, October, November, and December 1979; January, March, and April 1980. Visits to Kure occurred in November 1979, March 1980, and October 1980. Biologists were stationed in a field camp on Laysan Island (Fig. 1) and collected food samples March–August 1979 and March–August 1980. Biologists manned a field station at Tern Island (French Frigate Shoals) and collected samples from July 1979 until December 1980. A biologist on Kure obtained samples March–April 1978 and March–April 1979. A 1-day visit to French Frigate Shoals occurred in January 1979. Visits to various islands offshore of the windward Oahu coast took place in July 1978, May 1979, November 1979, July 1980, and November 1980. It is the nature of work in a study area as remote as the NWHI that collecting visits were opportunistic and sampling design could not be entirely controlled by the investigators.

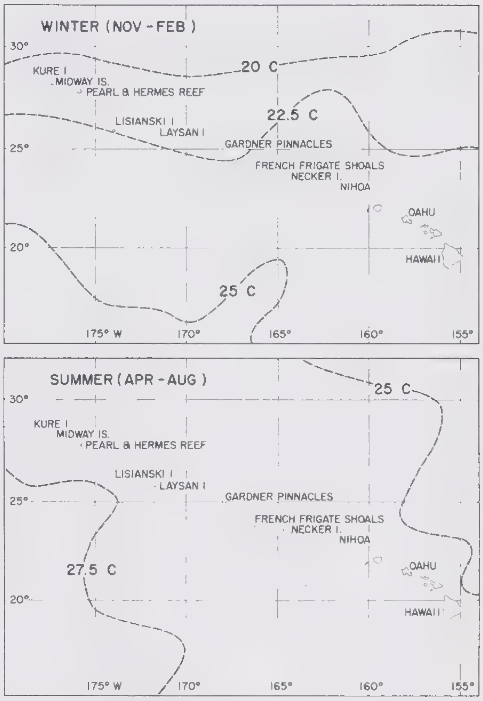

Fig. 1. The Hawaiian Archipelago with winter and summer surface isotherms from Armstrong (1973).

We intended to sample food habits of all species on each island during each 3-month season, but this proved impossible because of personnel limitations and the inherent inaccessibility of many islands. Nihoa, Necker, Laysan, Lisianski, and Pearl and Hermes Reef could be visited only on an expedition supported by a large vessel. Bad weather precluded landing on certain islands during scheduled cruises. Furthermore, many species occur only seasonally in the NWHI. For example, Laysan and black-footed albatrosses were present only November–July, sooty storm-petrels were present only January–May, and gray-backed terns were present only March–June. Several species have a limited distribution within the study area. Blue-gray noddies are found only on 4 islands (Table 1), and 2 of these (Gardner Pinnacles and La Perouse Pinnacle [French Frigate Shoals]) were inaccessible. Consequently, sampling of this species was limited to Nihoa and Necker Islands at times when vessel support was available and weather conditions permitted making the hazardous landings.

Finally, the presence of birds on an island did not insure that samples could be obtained. Laysan albatrosses present in July were mostly fledglings living off fat reserves, whereas those present in November were adults setting up breeding territories and establishing pair bonds (Fisher and Fisher 1969). In both cases, birds present on the islands appeared to contain no food during those months. Courting, nonfeeding adults of Bonin petrels, red-tailed tropicbirds, and great frigatebirds were also present. Few black noddy food samples were obtained from Midway or Kure because this species roosted high in ironwood trees (*Casuarina equisetifolia*), and live capture was rarely possible. Similar problems in food collection occurred with black noddies on Nihoa and Necker where roosting sites were faces of sheer cliffs.

We generally captured birds alive by hand or with a long-handled polypropylene fish net (Ashmole and Ashmole 1967*b*). Some populations on some islands were small (Table 1), and killing individuals for this study was undesirable (Tomback 1975).

We sampled adults, chicks, and immature birds. Upon capture, each bird was turned upside down. If the bird did not regurgitate immediately, it was squeezed or shaken. We quickly learned to determine when a bird in hand was likely to produce a food sample using weight, size, and distention as criteria. We found that food samples were most easily obtained during periods when parents were feeding young. Young of all species readily regurgitated when handled, and adults feeding young usually regurgitated when captured on the colony. The observation of a parent feeding a nestling was often used to indicate which bird to sample in order to economize effort in the field. Additionally, collections in the late afternoons and early evenings gave samples of better condition more readily than at other times of the day. Samples were taken at all hours of the day, but efforts were maximized from 1600–2100 hours. Samples that were too digested to be identifiable were often discarded in the field.

All pelecaniforms regurgitated readily if they contained food, and empty birds often regurgitated digestive juice. Terns readily regurgitated or dropped (white terns) samples for this study. The 7 procellariiforms presented the greatest sampling problems. Adult albatrosses rarely regurgitated, but chicks did immediately if recently fed. Christmas shearwaters and wedge-tailed shearwaters could be induced to regurgitate by holding the birds upside down and applying strong enough pressure to the abdomen to visibly stress the bird. Our initial samples from sooty storm-petrels, Bulwer's petrels, and Bonin petrels consisted only of oil or food so digested that only gross identification of prey items was possible. Attempts to induce Bonin petrels to regurgitate by use of emetics (e.g., Radke and Fryendall 1974, Tomback 1975) were unsuccessful. About 100 birds (wedge-tailed shearwaters, Bonin petrels, and Bulwer's petrels), many of which were empty, were sacrificed at the onset of the study to provide sample material.

Each sample was preserved in 10% formalin. Because isopropyl alcohol was not used as a preservative due to its less desirable quality of preserving fish for our identification techniques, we could not identify otoliths (Fitch and Brownell 1968). After failing to get many identifiable fish specimens from Bonin and Bulwer's petrels, a few samples were preserved in alcohol so that otolith identification could be made. Field data recorded include island, species, date, time, age of bird (adult, juvenile, nestling), sex of bird (if possible), and any additional comments that seemed pertinent.

Laboratory Procedures

The laboratory procedures used in processing the samples of seabird regurgitations were similar to those used by Ashmole and Ashmole (1967*b*), Reintjes and King (1953), and King and Ikehara (1956). The methods used by Schreiber and Hensley (1976) in their study of the diets of 3 pelecaniforms on Christmas Island differed from ours in that they analyzed only the fresh or slightly digested material. Additionally, they both weighed and measured the volume of individual prey items.

We poured each sample into a strainer, rinsed it with running water, and removed any objects not considered to be food items. Such objects included sand, twigs, leaves, flies, strands of monofilament line, plastic chips, pumice, and styrofoam pieces. These items were weighed for a subset of the albatross samples. The densities of such objects are extremely variable, and volumes would have been misleading.

We frequently found clusters of fish eggs attached to floating objects in samples taken from Laysan and black-footed albatrosses. We removed the clusters and treated the thousands of eggs as a single mass. Prey items were segregated into major groups and then identified to the lowest taxon possible.

We recorded the number of individuals of each taxon. In many instances we had to make a decision regarding what to count. For example, we encountered a large number of chitinous squid beaks that "resist attack by the digestive juices in the stomach for some time after other tissues have been digested" (Clarke 1977:92). We followed the method of Pinkas et al. (1971) and counted either upper or lower beaks, using the count with the highest number. Although the time it took the predator to accumulate all of the squid beaks is unknown, we believe it is important to show that many squids were consumed. Squid beaks have been enumerated differently by various investigators. Imber (1973) in his study of the food of gray-faced petrels counted the number of lower squid beaks. Ashmole and Ashmole (1967*b*) counted all squid beaks in a sample as 1 squid. Fish remains and invertebrate remains were enumerated as 1 whenever the actual number of individuals could not be determined. Frequently the posterior parts of a fish persisted although the head and otoliths were digested. Swallowing fish head first has been recorded by Imber (1973) and is an apparent adaptation to prevent a bird from being impaled by the spines and rays (Gochfeld 1975). Fish counts were based on the number of caudal peduncle-hypural fan sections that were present whenever heads were separated from tail sections or when there were fragments of fishes.

Volumes were determined by water displacement using a graduated cylinder. The smallest volume used in our analyses was 0.1 ml. This presented a problem with copepods and sea-striders because 0.1 ml is greater than their true volume. However, the volumes of most of the tiny prey items were measured in aggregate so that there was no gross distortion of volume.

Length measurements of prey items were made whenever possible. The lengths of most fishes were measured from the tip of the snout to the tip of the hypural fan (standard length). The lengths of marlins and needlefishes (scientific names of fishes are given in Appendix 2) were measured from the nostril to the tip of the hypural fan. The accuracy of the measurements were ranked as grade 1 for precise and grade 2 for slightly estimated. Grade 2 fish lengths were good measurements where only a small part of the fish was missing, i.e., the snout or hypural fan. Grade 3 fishes had a larger portion of the body missing and were rough estimates. Grade 4 fishes had most of the body missing and the length was estimated.

Mantle lengths were measured for the squids and total lengths for isopods. For

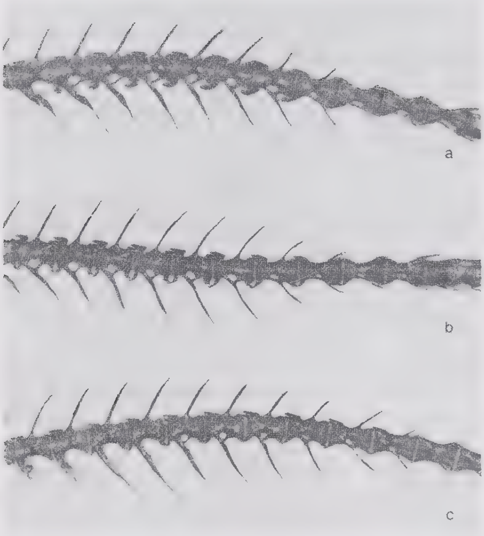

Fig. 2. Vertebral comparisons for *Decapterus macrosoma* (a), *D. tabl* (b), and *D.* sp. (c).

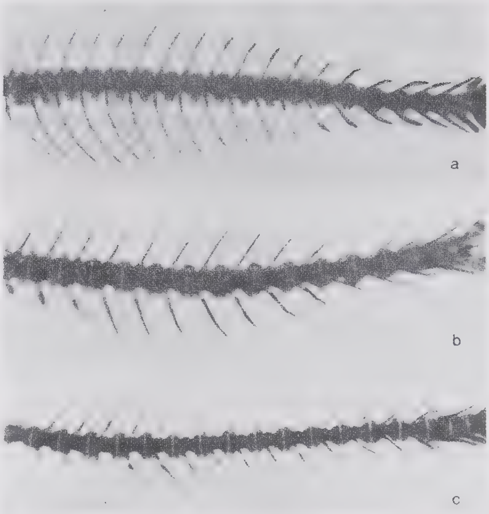

Fig. 3. Vertebral comparison of *Coryphaena equiselis* (a), *Seriola* sp. (b), and *Naucrates ductor* (c).

odd-shaped organisms such as medusae and wind-sailers, we measured the largest diameter.

The stage of digestion of prey items was graded as 1 for fresh, 2 for slightly digested, 3 for advanced state of digestion, and 4 for bone, squid beak, or exoskeleton remains. We assigned grade 5 to prey that was semidehydrated or dehydrated. The latter items were always dropped by white terns, which are well-known for carrying food to young lengthwise in the bill (Stonehouse 1962). In comparison to our method, Ashmole and Ashmole (1967*b*) recorded the fish and squid remains as grade 1 for those in good condition whose lengths could be measured accurately, grade 2 for those that were slightly broken or digested but fairly accurate measurements could be obtained, and grade 3 for items largely digested for which lengths were estimated.

The mean, minimum, maximum, and standard error for both length and volume have been presented for common items. We restricted those analyses to prey items in grades 1 and 2, but used all grades for frequency of occurrence and average percent volume.

We often found it necessary to assign a different grade for the length measurement than for the stage of digestion for a prey item. Very frequently a well-digested fish had its axial skeleton intact and a fairly accurate length measurement could be obtained. This was recorded as grade 3 for volume but grade 2 for length measurement because the length was reasonably accurate. We sometimes encountered fresh chunks of fish that appeared to have been chopped; these were graded 2 for volume but 4 for length. We considered parasitic isopods (crustacean ectoparasites) to be part of the host and processed them as such rather than as independent prey items. However, when an ectoparasite occurred alone, it was processed as a food item. Ashmole and Ashmole (1967*b*) treated the crustacean ectoparasites of fish as food items when they occurred in a sample, stating that some of the prey items in their samples may have come from the stomach of a larger prey item but was recorded as prey of the seabird. We agree that food consumed by a prey species may

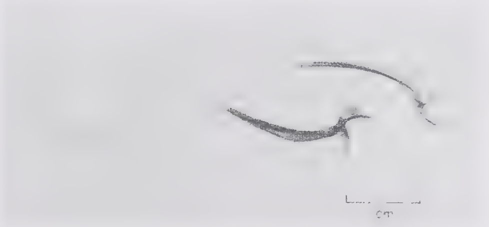

Fig. 4. The cleithrums of 2 hatchetfishes.

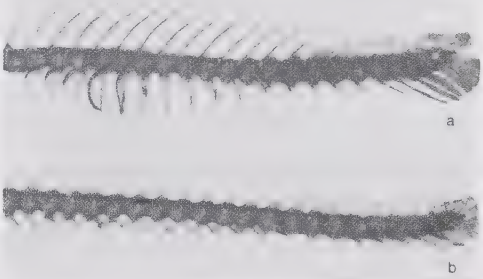

Fig. 5. Vertebral comparison of a flyingfish (a) and a halfbeak (b).

confound the results of any food study, but it was a minor problem here.

Prey Identification

A wide variety of prey items that included 78 fish species belonging to 56 families, 9 groups of crustaceans, and 7 squid families encountered in various stages of digestion made identification a challenge. Prey items ranged in size from tiny sea-striders and copepods measuring a few millimeters and displacing <0.1 ml to adult flyingfishes, juvenile tunas, and juvenile dolphin-fishes measuring >340 mm and displacing >300 ml. Very often the prey items were so well digested that only a few loose bones or squid beaks remained. A reference collection of fish axial skeletons was made during the course of the laboratory work to help identify the fishes. Many fishes could not be identified because key identifying characters were missing and the reference collection was inadequate.

Fish vertebrae were prepared by removing the flesh from either the whole fish or 1 side of the fish and subsequently staining it with Alizarin S, a water soluble bone stain. A weak concentration of stain was used when soaking overnight to bring out the finer configurations of the zygapophysis and other bony parts whereas a stronger concentration was used for quick staining to facilitate the counting of vertebrae, fin rays, and spines.

The vertebrae of 3 *Decapterus* spp. are compared in Fig. 2. The haemal post-zygapophysis is overlapped by the haemal pre-zygapophysis of the posterior vertebrae in *D. macrosoma*, and the high neural zygapophysis and presence of the first inferior vertebral foramina on the first caudal vertebra identifies *D. tabl* (R. L. Humphreys, pers. commun.). The other vertebra illustrated represents either *D. muroadsi* or *D. macarellus*. We lack *D. muroadsi* specimens that would aid recognition of vertebral differences between these 2 species.

The similar vertebrae of *Coryphaena equiselis*, amberjacks, and pilot fish can be distinguished (Fig. 3). In some cases, the presence of just a few pieces of flesh and a bone such as the cleithrum of the hatchetfishes could be adequate to identify the prey item to family or genus (Fig. 4). The shape of spines in the area of the caudal peduncle helped to distinguish flyingfishes from halfbeaks (Fig. 5). The young of a swordfish (*Xiphias gladius*) was identified using its unique spined scales. Potthoff and Richards (1970) used adult characteristics and features of the axial skeleton to aid in their identification of scombrids.

Squids were identified by use of their locking mechanisms, pens, and luminous organs. Squid beaks were not identified because there are no reliable keys for Hawaii (R. E. Young, pers. commun.). The identification of squids in the Hawaiian area is still incomplete, and it would take a major effort to collect specimens of all species and size ranges. Some researchers

(Imber 1973) have identified squid beaks using Clarke's (1962) key and illustrations.

Crustaceans pose less of a problem of identification because of their digestion-resistant exoskeleton (Reintjes and King 1953, Imber 1973). Identification to order usually presented very little problem, but further identification depended upon the condition of the prey item. Copepods were usually identifiable to genus or species because their exoskeletons remained fairly intact.

Numerous keys and guides were consulted to identify the prey items. The most useful were Wilson (1932), Rose (1933), Townsley (1953), Gosline and Brock (1960), Matsumoto (1963, 1967), Strasburg (1964), Nakamura and Kikawa (1966), Collette et al. (1969), Lindberg and Legeza (1969), Lindberg and Krasyukova (1971), Ovchinnikov (1971), Tinker (1978), and Tyler (1980).

Data Analysis

The data are presented as numerical abundance, volume, and frequency of occurrence. The use of these 3 kinds of data is widespread in food studies in the marine environment, and we agree that each measures a different yet important aspect of prey utilization (Reintjes and King 1953, Waldron and King 1963, Ashmole and Ashmole 1967*b*). Reintjes and King (1953) stated that each individual method has shortcomings but that a prey item that ranks high in number, volume, and frequency of occurrence is important at the time and place sampled.

Various combinations of these basic types of data have been used to achieve a single ranking of the importance of prey items because the repetition of each becomes cumbersome in a textual discussion. We adopted the ranking method used by Waldron and King (1963) and Ashmole and Ashmole (1967*b*) but modified their method of calculating volume. We ranked prey organisms separately in terms of number, volume, and frequency of occurrence. We then summed and arranged these 3 subrankings in a single sequence from lowest to highest to produce a final ranking for each prey taxon. This ranking method weights each method equally. Our method gives equal weight to each sample by summing the volumetric percentage of each item and dividing by the sample size to arrive at an average percentage volume. The aggregate total volume method (Ashmole and Ashmole 1967*b*) weights large-sample volumes more than small-sample volumes, and a 200-ml sample would have twice the weight of a 100-ml sample. We compared our ranking method for several seabird species with the one used by Pinkas et al. (1971) and found only minor differences in rank for highly ranked prey items.

The ranking of prey taxa gives a good idea of their relative importance in the diet without excessive attention to an illusory sense of precision, which can come, for example, from a strict comparison of numerical or volumetric data. Matthews et al. (1977) stated that the number of taxa from any 1 category of forage items should not be considered quantitatively because of the differences in taxonomic level to which the prey items were identified. The rankings for prey items by families or major groups show which are relatively the most important. The list of genera and species gives an idea of which species are important within the family or group. It must be noted that the categories of unidentified fishes and unidentified remains rank high because they are a composite of unidentified material presumably from many species, which by necessity have been pooled together. It is unlikely that for any seabird "unidentified fishes" refers to a single species.

We analyzed the data by grouping adjacent islands. The Midway Island group also included Kure Island and Pearl and Hermes Reef. The Laysan Island group included Lisianski Island. The French Frigate Shoals group also included Necker and Nihoa Islands. For each group, the data were analyzed using winter (Jan–Mar), spring (Apr–Jun), summer (Jul–Sep),

Table 2. Weights and bill measurements of Hawaiian seabirds from this study.

	Wt (g)[a]					Bill (cm)				
Species	*N*	$\bar{x}$	SE	Range	Months	*N*	Culmen length[b]	SE	Width[c]	SE
Black-footed albatross	84	2,820	64	2,025–3,800	Apr–Jun	10	10.40	0.12	3.25	0.04
Laysan albatross	87	2,410	31	1,900–3,075	Apr–Jun	10	11.10	0.12	3.26	0.04
Bonin petrel	168	176	1	150–220	Mar–Oct	10	2.61	0.03	1.11	0.02
Bulwer's petrel	191	99	1	78–130	Apr–Aug	10	2.04	0.04	0.74	0.01
Wedge-tailed shearwater	124	388	3	320–510	May–Aug	10	3.94	0.07	1.19	0.02
Christmas shearwater	99	356	3	280–415	Apr–Aug	10	3.23	0.04	1.01	0.02
Sooty storm-petrel	61	84	1	66–105	Apr–May	20	1.80	0.05	0.93	0.02
Red-tailed tropicbird	84	624	5	540–750	Apr–Aug	10	6.09	0.07	2.00	0.08
Masked booby	132	2,160	18	1,770–2,800	Apr–Aug	10	11.50	0.09	3.00	0.04
Red-footed booby	80	1,110	12	905–1,400	Apr–Aug	10	8.38	0.10	2.57	0.04
Brown booby	43	1,340	18	1,050–1,775	Jun–Sep	10	12.47	0.15	3.30	0.03
Great frigatebird	117	1,440	13	1,060–1,950	Apr–Aug	10	10.90	0.20	3.13	0.07
Sooty tern	94	198	3	153–320	Apr–Jul	10	4.68	0.08	0.99	0.02
Gray-backed tern	83	146	1	115–177	Apr–Aug	10	4.26	0.05	1.00	0.02
Brown noddy	99	205	2	153–275	Apr–Aug	10	4.62	0.05	1.11	0.02
Black noddy	86	108	1	85–133	Apr–Sep	10	4.76	0.08	0.90	0.02
White tern	109	111	1	92–139	May–Sep	20	4.34	0.04	0.79	0.02
Blue-gray noddy	52	53	1	46–65	Jun	30	2.55	0.02	0.81	0.02

[a] Weights from Laysan Island except some Bonin petrel weights were from Midway Islands and all blue-gray noddy weights were from Necker and Nihoa Islands

[b] Length from tip to angle of gonys.

[c] Proximal end of gonys.

and fall (Oct–Dec). These groupings were necessary because we obtained insufficient samples to compare each month and each island.

Prey lengths for common prey items were compared using analysis of variance (ANOVA). Means and standard errors were calculated for weight, bill width, and culmen length of each seabird species.

RESULTS

Weights and bill measurements (Table 2) indicate that Hawaiian species are similar to those studied elsewhere. However, except for the red-tailed tropicbird, each species, for which a comparison can be made with Christmas Island (Ashmole and Ashmole 1967*b*:18, Schreiber and Hensley 1976:245), is heavier in the NWHI (Table 2). The significance of this difference bears further study.

Most seabirds in this community feed most of their young during spring and summer (Fig. 6). There are several exceptions, however. Four procellariiforms and the black noddy feed nestlings during winter.

Species Accounts

The species are treated in order of decreasing body weight, following Ashmole and Ashmole (1967*b*).

Black-footed Albatross.—We collected and analyzed 172 black-footed albatross samples from 1978–80. Most were from Laysan and Midway Islands, but we also collected at Kure and French Frigate Shoals. Samples were collected from February, when chicks hatch, until June, when young are abandoned by their parents. Obtaining food samples from adult birds proved to be difficult. Consequently 84% of the samples were taken from chicks, and the remainder were taken from adults. The samples averaged 96 ml and contained an average of 15 items. The samples generally were in poor condition, even when obtained from adult birds or chicks

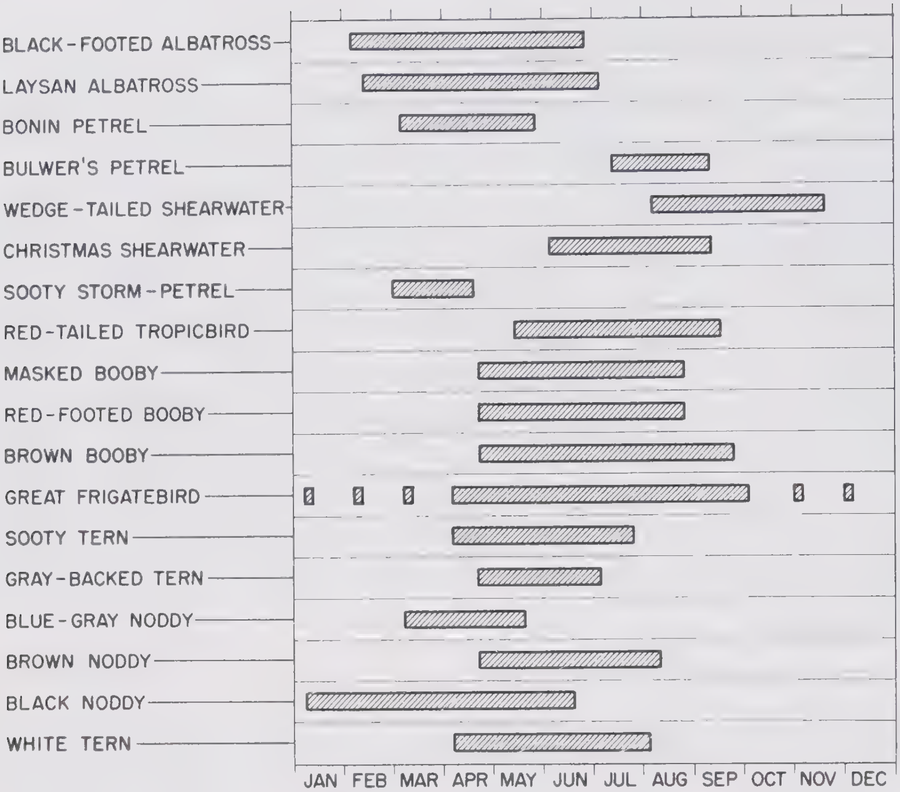

Fig. 6. Maximum feeding periods for dependent young of Hawaiian seabirds, representing about 80% of the feeding activity. Great frigatebirds feed dependent young throughout the year.

that had just been fed by an adult returning from sea. Consequently, identification of prey beyond family level was very difficult.

Prey consisted of 4 fish families, 3 squid families, an octopus, 8 crustacean groups, and a variety of other objects (Table 3). Samples also contained many floating objects, some of which provided a substrate for flyingfish ova (Table 4). About 10% of the volume of black-footed albatross samples was stomach oil, a common feature of procellariiformes (Imber 1976, Warham et al. 1976). Our laboratory analysis excluded the oil and found prey to be 50% fish, 32% squid, and 5% crustacean by volume. Common food items throughout the sampling period were squid, especially Ommastrephidae, and flyingfish ova. The high ranking of unidentified remains, unidentified crustaceans, and unidentified fishes gives an indication of the poor condition of samples (Table 3). However, it is probable that most important taxa are included in the species list. Squid rank particularly high due to the frequent occurrence of digestion-resistant beaks (as many as 66 in 1 sample). Although Imber (1973) identified squid from their beaks, we made no effort to identify ours because no suitable reference collection of beaks exists for the NWHI. Flyingfish ova were the most important prey item by volume (44%), and each egg mass was counted as a single prey item. The abundance in the diet of certain large crustaceans was unexpected, because they are believed to inhabit only very deep water. These include the mysids *Gnathophausia gigas* and *G. ingens*, the isopod *Anuropus branchiatus*, the leptostracan *Nebaliopsis typica*, and the shrimp *Notostomus japonicus*.

Table 3. Prey items identified to lowest taxon in 172 black-footed albatross samples. Prey items were ranked separately in terms of number, volume, and frequency of occurrence. These 3 subrankings were summed and arranged in a single sequence from lowest to highest to achieve the rank reported here for each prey taxon.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Carangidae	19			
Decapterus sp.		1	0.6	0.3
Exocoetidae	2			
Exocoetidae (ova)		139	80.2	44.2
Unidentified exocoetid		7	4.1	1.8
Gempylidae	19	1	0.6	0.3
Sternoptychidae	23.5	1	0.6	0.1
Unidentified fishes	6	24	13.4	3.0
SEABIRDS	13			
Puffinus sp.		1	0.6	0.1
P. pacificus		1	0.6	0.2
Pterodroma hypoleuca		1	0.6	0.1
MOLLUSCA				
Decapoda				
Ommastrephidae	4			
Symplectoteuthis oualaniensis		1	0.6	0.2
Hyaloteuthis pelagicus		1	0.6	<0.1
Unidentified ommastrephid		47	10.5	3.2
Cranchiidae	23.5	1	0.6	<0.1
Octopoteuthidae	19	1	0.6	0.3
Unidentified squid	1	2,182	91.9	28.1
Octopoda	17	2	0.6	0.2
CRUSTACEA				
Mysidacea	7			
Gnathophausia spp.		5	2.3	0.1
G. gigas		6	3.5	0.9
G. ingens		1	0.6	<0.1
Unidentified mysid		4	2.3	0.1
Euphausiacea	23.5	1	0.6	<0.1
Amphipoda	12			
Alicella sp.		1	0.6	0.4
Unidentified amphipod		2	1.2	0.1
Isopoda	10			
Anuropus sp.		1	0.6	0.1
A. branchiatus		3	1.7	0.8
Parasitic isopod		1	0.6	<0.1
Unidentified isopod		1	0.6	<0.1
Nebaliacea	23.5			
Nebaliopsis typica		1	0.6	<0.1
Copepoda	11			
Penella spp.		17	1.7	0.1
Shrimp	8.5			
Oplophoridae				
Notostomus spp.		2	1.2	<0.1
N. japonicus		2	1.2	0.1
Unidentified oplophorid		1	0.6	<0.1
Pasiphaeidae		3	1.7	0.1
Unidentified shrimp		5	2.9	0.3
Crab	14			
Brachyura		6	2.3	<0.1
Grapsidae				
Planes cyaneus		1	0.6	<0.1
Unidentified crustacean	5	39	22.1	1.2
INSECTA				
Gerridae	15			
Halobates sericeus		5	1.2	<0.1
Caterpillar	23.5	1	0.6	<0.1
COELENTERATA				
Velellidae	16			
Velella velella		1	0.6	0.6
TUNICATA				
Pyrosomatidae	8.5	15	4.7	0.5
ALGAE				
Sargassum sp.	23.5	1	0.6	<0.1
UNIDENTIFIED REMAINS	3	51	29.7	11.1
UNIDENTIFIED MEAT		3	1.7	0.9

Measured lengths of intact prey ranged from a 4-mm sea-strider to a 300-mm amphipod, the latter probably being the largest known (Barnard and Bowman, pers. commun.). Most length measurements were ommastrephid squids ($\bar{x} = 74$ mm, Table 5). Some crustaceans were longer than the squids. *G. gigas* and *A. branchiatus* averaged 112 and 106 mm, respectively. Length data of prey of this species must be interpreted with some caution. They often feed in groups and have strong bills capable of ripping and tearing flesh. It is probable that many of the squid fragments occurring in the samples were not taken whole but were shredded from individuals much larger than those that we were able to measure or that an albatross could swallow whole. Squid arms of at least 200 mm were found next to albatross nests on Midway and Laysan Islands, apparently too large for the young to swallow. The mantles from such individuals were certainly much larger than 120 mm, the largest ommastrephid squid that we measured (Table 5). Flyingfish ova clusters averaged 86 ml and appeared to be relatively fresh, perhaps indicating a resistance to digestion. The largest egg mass displaced 301 ml and weighed 314 g. We estimated that it contained more than 156,000 ova. Most diameters of in-

Table 4. Weights and percent of sample by weight of indigestible items in 14 black-footed and 12 Laysan albatrosses.[a]

Species	Mean wt of indigestible items (g)	SE	Percent of sample by wt	SE
Black-footed albatross	9.9	1.7	12.2	2.6
Laysan albatross	10.6	3.2	14.7	5.2

[a] Both species contained squid beaks, squid lenses, plastic chips, styrofoam, pumice, and monofilament. The black-footed albatross also yielded rubber, sponges, and a paper wrapper. The Laysan albatross additionally yielded bird bones and a kukui nut (*Aleurites moluccana*).

dividual ova were 1.5–1.7 mm, but some were as large as 2.3 mm.

There were few differences in the major prey items consumed by this predator between either winter and spring or among any of the 3 island groups of the NWHI. During winter and spring, squid and egg masses of flyingfishes were the first and second ranked prey items in each island group. This order was reversed during spring in the French Frigate Shoals region, but the number of samples collected there was relatively low, and we attach no importance to this difference.

These results generally correspond to anecdotes concerning the feeding habits of this species, where it has been reported to feed on flyingfishes (Fisher 1945), shrimps (Anderson 1954), squids, gammarids, sea urchins (Cottam and Knappen 1939), fish eggs, sun fish, and algae (Miller 1940). The black-footed albatross is so renowned for its habit of following ships and feeding on refuse that Miller (1940) referred to it as the "feathered pig."

Laysan Albatross.—We collected 183 samples from Laysan albatrosses from 1978–80 with samples taken from Laysan, Midway, Kure, and French Frigate Shoals. Samples were collected February–July when chicks were being fed by parents. Food samples from adult birds were particularly difficult to obtain from this species, and more than 95% of our samples came from chicks. Sample volumes averaged 64 ml and contained a mean of 32 items. Samples generally were in an advanced state of digestion, which limited our ability to identify and measure prey items.

We identified 9 fish families, 6 squid families, a gastropod, 8 groups of crustaceans, an insect, a coelenterate, and a tunicate as prey (Table 6). Plastic particles, styrofoam, and pumice were regularly obtained from Laysan albatrosses, but we kept records of nonfood items from only a portion of our samples (Table 4). Kenyon and Kridler (1969) also found large amounts of indegistible matter, especially plastics, in stomachs of Laysan albatrosses. As with the black-footed albatross, about 10% by volume consisted of stomach oil that we ignored in the laboratory analysis. We found the prey to be 9% fish, 65% squid, 9% crustaceans, and 4% coelenter-

Table 5. Lengths and volumes of some prey items[a] of the black-footed albatross. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Exocoetidae ova		48		1.4		301		86		10
MOLLUSCA										
Ommastrephidae	42		36		120		74		3	
CRUSTACEA										
Gnathophausia gigas	3		80		140		112		17	
Anuropus branchiatus	3		94		115		106		6	
TUNICATA										
Pyrosomatidae	5		29		72		48		7	

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods)

Table 6. Prey items identified to lowest taxon in 183 Laysan albatross samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organ- isms	Percent of samples in which oc- curred	Avg % vol
FISHES				
Exocoetidae	4.5			
Cypselurus sp.		1	0.5	0.5
Exocoetidae (ova)		20	10.9	3.6
Unidentified exocoetid		6	2.7	0.1
Gempylidae	27	1	0.5	0.1
Gonostomatidae	23			
Vinciguerria spp.		6	0.5	<0.1
Hemiramphidae	19			
Euleptorhamphus viridis		1	0.5	0.1
Unidentified hemiramphid		2	1.1	<0.1
Molidae	13			
Ranzania laevis		12	2.2	0.9
Unidentified molid		2	1.1	0.7
Mullidae	28.5	2	0.5	<0.1
Myctophidae	20	5	2.7	<0.1
Scomberesocidae	12			
Cololabis saira		13	4.4	0.5
C. saira (ova)		3	1.6	<0.1
Sternoptychidae	31			
Argyropelecus sp.		1	0.5	<0.1
Unidentified fishes	8	24	12.6	2.1
MOLLUSCA				
Decapoda				
Ommastrephidae	2			
Symplectoteuthis spp.		4	1.1	0.5
S. oualaniensis		2	1.1	0.9
Unidentified ommastrephid		196	26.8	14.6
Lepidoteuthidae	18	2	1.1	0.9
Mastigoteuthidae	26			
Mastigoteuthis sp.		1	0.5	0.3
Enoploteuthidae	31			
Thelidioteuthis alessandrinii		1	0.5	<0.1
Onychoteuthidae	21	3	0.5	0.3
Histioteuthidae	25	1	0.5	0.4
Unidentified squids	1	3,224	82.5	46.6
Janthinidae	15			
Janthina sp. (ova)		5	2.7	1.8
Unidentified mollusk	22	3	1.1	0.1
CRUSTACEA				
Mysidacea	7			
Gnathophausia spp.		12	4.4	1.0
G. gigas		3	1.1	0.1
G. ingens		7	2.7	0.9
Unidentified mysid		4	2.2	0.3
Euphausiacea	17	1,415	0.5	0.1
Stomatopoda	31			
Pseudosquilla sp.		1	0.5	<0.1
Amphipoda	14			
Eurythenes gryllus		1	0.5	<0.1
Unidentified amphipod		8	3.8	0.6
Isopoda	10			
Anuropus sp.		1	0.5	0.1
A. branchiatus		12	6.0	1.2
Parasitic isopod		1	0.5	0.5
Unidentified isopod		3	1.6	<0.1
Nebaliacea	24			
Nebaliopsis typica		2	1.1	<0.1
Shrimp	9			
Caridea		2	1.1	0.1
Oplophoridae		3	1.6	<0.1
Notostomus spp.		4	2.2	0.2
Acanthephyra sp.		1	0.5	<0.1
A. exima		1	0.5	0.3
Pasiphaeidae		2	1.1	<0.1
Unidentified shrimp		11	5.5	0.3
Crab	16			
Brachyura		3	1.6	0.1
Grapsidae				
Planes cyaneus		11	2.2	<0.1
Unidentified crustacean		56	27.9	2.8
TUNICATA				
Pyrosomatidae	11	25	4.4	0.6
INSECTA				
Gerridae	28.5			
Halobates sericeus		2	0.5	<0.1
COELENTERATA				
Velellidae	6			
Velella velella		668	9.8	4.0
UNIDENTIFIED REMAINS	3	67	32.2	10.8

ates by volume. Squids (especially Ommastrephidae), flyingfishes, wind-sailers, and mysids (*G. gigas* and *G. ingens*) were the highest ranking prey items (Table 6). The ranking of unidentified crustaceans, fishes, and other remains within the top 8 categories underscores the poor sample condition. Laysan albatrosses very frequently ate squid, which occurred in 93% of our samples. Flyingfishes (including ova), the next highest ranked prey, occurred in only 13% of our samples and accounted for only 4% of the volume of the prey (Table 6). By-the-wind sailors ranked below flyingfishes, occurring in <10% of the samples and accounting for 4% of the prey volume. Mysids of both *Gnathophausia* species and the isopod *Anuropus branchiatus* were not expected to be prey because they are believed to occur only in very deep water. Because Laysan albatrosses are surface feeders, these crustaceans must occur regularly in surface waters.

Table 7. Lengths and volumes of some prey items[a] of the Laysan albatross. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Exocoetidae ova		6		3.4		195		44		30
MOLLUSCA										
Ommastrephidae	155		28		144		71		2	
Symplectoteuthis spp.	4		77		92		86			3
CRUSTACEA										
Anuropus branchiatus	7		49		840		187		109	
Planes cyaneus	11		8		17		10		1	
Amphipoda	7	2	12	0.2	58	0.7	28	0.4	6	0.3
TUNICATA										
Pyrosomatidae	15		21		80		39		5	

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

Only 229 prey items were sufficiently intact to measure, and they ranged from an 8-mm crab to a 150-mm mysid. Most measurements were of ommastrephid squids, which averaged 71 mm in length (Table 7). We were unable to obtain length or volume data from any fish prey. We did measure the volumes of flyingfish ova masses that averaged 44 ml. Prey length data from a species that is known to shred its prey before ingestion must be interpreted with caution. Squid arms on Laysan albatross colonies were found that must have come from much larger individuals than the largest squid (144 mm) that we were able to measure. Okutani and Ih-Hsiu (1978) stated that *Symplectoteuthis oualaniensis* (Ommastrephidae) attains lengths >460 mm. In addition, some of the large beaks that we found probably came from very large squids.

Our rankings of prey items of the Laysan albatross showed only minor variation among island groups or seasons. In all 3 regions, unidentified or ommastrephid squids were the highest ranked prey during both winter and spring. Wind-sailers ranked high in the Midway region during spring but not winter and in the Laysan region during winter but not spring. This prey item did not occur in the French Frigate Shoals region. Pacific sauries were consumed both as fish and as egg masses. They ranked high only during winter in the Midway region and did not occur during spring. They occurred sporadically in samples from other regions. Mysids were generally found January–June in each of the 3 regions but proved to be especially common in the diet of the Laysan albatross during this period in the French Frigate Shoals region and during spring at Midway.

Our results corroborate earlier qualitative reports that this species feeds on squids (Fisher 1904), shrimps, and fish roe (Anderson 1954). Kenyon and Kridler (1969) identified squid beaks from Octopodoteuthidae and Onychoteuthidae in addition to Ommastrephidae.

Masked Booby.—We obtained 305 samples from masked boobies from most of the islands within the Hawaiian Archipelago but predominantly from French Frigate Shoals, Laysan, and Kure. Samples were collected March–November. Samples were obtained easily from adults (76%), subadults (7%), and nestlings (16%). Pooling all samples collected 1978–80, the mean volume was 167 ml, and there was a mean 2.5 prey items/sample. Samples from masked boobies generally were in good condition. More than 97% of the fishes from these samples were identified to family and more than 65% to genus or species.

Fish constituted over 97% of the sample volumes with squid comprising the re-

Table 8. Prey items identified to lowest taxon in 305 masked booby samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Belonidae	11			
Platybelone argalus platyura		3	0.7	0.1
Ablennes hians		1	0.3	<0.1
Unidentified belonid		1	0.3	<0.1
Carangidae	2			
Decapterus spp.		126	25.6	22.7
D. macarellus		10	2.0	1.7
D. macrosoma		71	6.2	4.6
Cirrhitidae	18.5			
Cirrhitops fasciatus		1	0.3	<0.1
Coryphaenidae	5			
Coryphaena spp.		2	0.7	0.1
C. hippurus		3	1.0	0.7
C. equiselis		16	3.0	2.0
Echeneidae	17	2	0.3	0.1
Exocoetidae	1			
Parexocoetus brachypterus		21	2.3	1.0
Exocoetus volitans		45	6.2	3.7
Cypselurus spp.		89	26.2	22.7
C. speculiger		6	2.0	0.8
C. atrisignis		1	0.3	0.3
Unidentified exocoetid		202	43.9	29.5
Gempylidae	14			
Gempylus serpens		3	1.0	<0.1
Hemiramphidae	3.5			
Euleptorhamphus viridis		31	7.2	2.7
Unidentified hemiramphid		4	0.7	0.1
Istiophoridae	13			
Tetrapterus angustirostris		1	0.3	<0.1
Unidentified istiophorid		1	0.3	<0.1
Kyphosidae	9			
Kyphosus bigibbus		6	1.3	0.6
Mullidae	10	10	1.3	0.1
Nomeidae	12			
Psenes cyanophrys		3	0.7	0.1
Pomacentridae	15	1	0.3	0.3
Scomberesocidae	16			
Cololabis saira		2	0.3	0.1
Scombridae	7			
Auxis thazard		2	0.7	0.7
Katsuwonus pelamis		6	1.6	1.5
Unidentified fishes	6	18	5.9	0.8
MOLLUSCA				
Decapoda				
Ommastrephidae	3.5			
Symplectoteuthis spp.		6	1.3	0.2
S. oualaniensis		4	0.7	0.1
Hyaloteuthis pelagicus		2	0.3	<0.1
Unidentified ommastrephid		58	8.5	2.2
Unidentified squids	8	12	2.6	0.1
UNIDENTIFIED REMAINS	18.5	1	0.3	<0.1

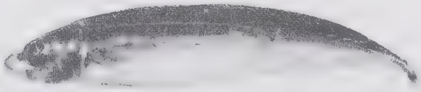

Fig. 7. *Decapterus* sp., a prey item.

mainder. Fifteen fish families and a single family of squid were identified. Flyingfishes ranked highest among the prey items, followed by jacks, halfbeaks, squids (Ommastrephidae), and dolphin-fishes (Table 8). Many of the flyingfishes were identified, including *Cypselurus speculiger, C. atrisignis, Parexocoetus brachypterus,* and *E. volitans.* All carangids were *Decapterus* spp. (Fig. 7), with many identified as *D. macrosoma* or *D. macarellus* (Fig. 2). All of the halfbeaks identified were *Euleptorhamphus viridis.* Some of the squids were identified as *S. oualaniensis* and *Hyaloteuthis pelagicus.* All of the dolphin-fishes were genus *Coryphaena* with the preponderance being *C. equiselis* rather than *C. hippurus.*

Length measurements were taken for 193 prey items and ranged from a 29-mm hawk fish to a 343-mm flyingfish. The mean for all measured prey was 161 mm. The fishes with the longest mean lengths were *E. viridis* (276 mm), *Cypselurus* spp. (231 mm), and *D. macarellus* (207 mm) (Table 9). The lengths of ommastrephid squids averaged 90 mm. The few displacement volumes of prey that we measured averaged 51 ml and ranged from 0.7 to 220 ml.

The families of prey items that ranked high when all data were combined (Table 8) remained high when the data were separated into seasons and island groups. Flyingfishes and carangids were the 2 highest ranking families, with flyingfishes ranking higher during the first 6 months of the year and carangids ranking higher during the second 6 months. Similarly halfbeaks ranked higher than dolphin-fishes during March–June, but dolphin-fishes were higher than halfbeaks July–November. Ommastrephid squids ranked

Table 9. Lengths and volumes of some prey items[a] of the masked booby. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Decapterus macarellus	8	2	185	132	224	139	207	136	5	4
D. macrosoma	8		66		165		133		14	
Decapterus spp.	29	1	66	220	240	220	195	220	6	
Parexocoetus brachypterus	11	5	125	34	153	44	136	37	3	2
Exocoetus volitans	30	3	95	32	184	56	144	47	4	8
Cypselurus spp.	22	2	134	90	343	102	231	96	13	6
Euleptorhamphus viridis	9	1	169	53	301	53	267	53	14	
MOLLUSCA										
Ommastrephidae	35	4	46	8	1,280	18	90	12	3	2
Symplectoteuthis spp.	6	1	73	13	100	13	88	13	4	

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

higher throughout the year in the French Frigate Shoals region than elsewhere, and were common in the Laysan and Midway regions only during spring. Pacific sauries ranked third during winter in the Midway Island group. Large flyingfishes and *Decapterus* spp. dominated the diet of this booby throughout the seasons and areas studied, but some changes in order of ranking are evident.

The diet of this species in Hawaii is similar to that reported from Christmas Island (Pacific Ocean) (Schreiber and Hensley 1976) and Ascension Island (Stonehouse 1962, Dorward 1963*a*). However, the diet in Hawaii is unique in the importance of *Decapterus* spp.

Great Frigatebird.—We collected and analyzed 284 regurgitations from great frigatebirds, primarily from Midway, Laysan, and French Frigate Shoals. We obtained samples during all months except December and January when 1978–80 are combined. Adults (37%), subadults (17%), and nestlings (45%) were sampled. The samples averaged 104 ml and 4.5 prey items. More than 96% of the fishes were identified at least to family.

Sample volumes were 85% fish, 14% squid, and 1% juvenile sooty terns. Twenty-three fish families and a single squid family were identified. We found no crustaceans. The highest ranking prey were flyingfishes (Fig. 8). Most were too digested to permit identification but *Cypselurus* spp., *Exocoetus volitans*, and *Parexocoetus brachypterus* were the most common (Table 10) of those identified. The second ranked item was ommastrephid squids. Of the few that could be identified, all were *Symplectoteuthis*, including *S. oualaniensis* and *S. luminosa*. Ranking third was Carangidae, mostly *Decapterus*, especially *D. macrosoma*. *D. macarellus* was also identified but is presented in Table 10 as *D.* spp. until the vertebrae of this species can be distinguished from *D. muroadsi*. Other highly ranked prey items included unidentified squids, a filefish (*Pervagor spilosoma*), and halfbeaks. We found few sooty terns, but B. Flint (pers. commun.) observed hundreds taken during 1980–81 at Tern Island, French Frigate Shoals.

We obtained lengths from 248 prey items. They averaged 83 mm and ranged from a 12-mm cow fish to a 272-mm halfbeak. The flyingfishes *E. volitans* and *P. brachypterus* averaged 141 and 135 mm, respectively (Table 11). *Symplectoteuthis* spp. averaged 85 mm. The fact that great frigatebirds will take cow fish ($\bar{x} = 17$ mm) and filefish ($\bar{x} = 60$ mm) in addition to the much larger flyingfishes demonstrates wide flexibility in the size classes of prey that may be exploited (Table 11).

Sampling was adequate to allow comparison among seasons and among the 3 island groups in the NWHI. Flyingfishes ranked very high throughout the year in each island group, usually first or second. Ommastrephid squids also ranked high throughout the archipelago, but peaked during spring and were absent from the Midway region during summer. Carangids were not found in any of 43 samples collected in winter, occurred to a limited degree in spring, but ranked very high in summer and fall, especially at French Frigate Shoals. Dolphin-fishes were very important in the Midway region during summer but occurred rarely elsewhere. Halfbeaks ranked fairly high throughout the archipelago, apparently ranking highest February–June. Pacific sauries ranked high during winter in the Midway region, and filefish ranked high during summer in the Laysan region. Neither of these fishes occurred in other regions, nor in other seasons within the region where they were found. This demonstrates the ability of the great frigatebird to locally exploit whatever prey is available, which is usually flyingfishes and squids.

The reliance of this species on flyingfishes and squids has also been reported at Ascension Island (Stonehouse 1962), Aldabra Atoll (Diamond 1974*a*), and Christmas Island (Schreiber and Hensley 1976). Great frigatebirds in Hawaii consume more *Decapterus* spp. than other areas studied and may feed on fewer juvenile sooty terns (Beard 1939, Schreiber and Hensley 1976) than they do elsewhere.

Brown Booby.—We collected 244 regurgitations from brown boobies, primarily from Laysan and Kure, but including samples from Lisianski, Pearl and Hermes Reef, Oahu, and Nihoa. We combined samples collected 1978–80, including material from each month March–November. Samples were readily obtained from adults (22%), juveniles (8%), and nestlings (69%). Brown boobies often spontaneously regurgitate upon seeing a human intruder in their colony. The samples averaged 100 ml and 12 prey items. The condition of samples from this species were among the best in this study, resulting in greater than 98% of the fishes being identified to family or lower.

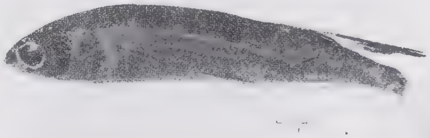

Fig. 8. Flyingfish, *Parexocoetus brachypterus*, a prey item.

Fish made up 95% of the sample volumes, and virtually all of the remainder was squid. Eighteen fish families, a single squid family, and an isopod were identified. The highest ranking family was Carangidae. Most of the fishes from this family were *Decapterus*, especially *D. macrosoma*, but large numbers of amberjacks and fair numbers of pilot fish, *Selar crumenophthalmus*, and *Caranx* spp. were found (Table 12). Ranking next were flyingfishes and juvenile goatfishes. No attempt was made to further identify any of the goatfishes, but 7 species of flyingfishes were identified. Ranking highest were *E. volitans* and *P. brachypterus* with *Cypselurus* spp. following very closely. Halfbeaks (especially *E. viridis*) and ommastrephid squids (especially *Ommastrephes* spp. and *Symplectoteuthis* spp.) ranked next.

The generally good condition of the samples allowed length measurement of 463 prey items. These items had a mean of 94 mm and ranged from a 3-mm isopod to a 319-mm halfbeak. The mean lengths of some common prey items include *D. macrosoma* (158 mm), goatfishes (54 mm), *E. volitans* (128 mm), rudderfish (81 mm), and Ommastrephidae (81 mm) (Table 13). Brown boobies exploit prey over a fairly wide range of lengths. Few prey items were considered intact enough to warrant the measurement of displacement volumes. The volumes we obtained averaged 25 ml, ranging from a 2-ml squid to a 68-ml halfbeak (Table 13).

An analysis of seasonal and geographical differences in this diet suffers from the fact that it was not feasible to collect sam-

Table 10. Prey items identified to lowest taxon in 284 great frigatebird samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Atherinidae	20			
Pranesus insularum		8	0.4	0.1
Balistidae	26	1	0.4	<0.1
Bramidae	26			
Brama orcini		1	0.4	<0.1
Carangidae	3			
Decapterus spp.		40	7.0	3.3
D. macrosoma		74	8.1	5.1
D. tabl		11	1.4	0.6
Selar crumenophthalmus		1	0.4	<0.1
Coryphaenidae	8			
Coryphaena spp.		4	1.1	0.5
C. hippurus		4	1.4	0.8
C. equiselis		4	1.4	0.5
Dactylopteridae	26			
Dactyloptena orientalis		1	0.4	<0.1
Exocoetidae	1			
Parexocoetus brachypterus		15	1.1	0.9
Exocoetus volitans		35	7.4	4.4
Cypselurus spp.		51	13.7	11.7
C. speculiger		1	0.4	0.2
C. simus		1	0.4	0.4
C. spilopterus		1	0.4	0.4
Unidentified exocoetid		346	61.6	42.5
Gempylidae	21			
Gempylus serpens		2	0.7	<0.1
Hemiramphidae	5			
Euleptorhamphus viridis		33	6.7	3.1
Oxyporhamphus micropterus		1	0.4	0.1
Unidentified hemiramphid		15	3.9	1.3
Istiophoridae	18			
Tetrapterus angustirostris		2	0.7	0.2
Kyphosidae	17			
Kyphosus bigibbus		4	0.7	0.2
Macrouridae	23	1	0.4	0.1
Molidae	16			
Ranzania laevis		2	0.4	0.2
Masturus lanceolatus		5	0.4	0.1
Monacanthidae	5			
Pervagor spilosoma		81	2.5	1.5
Unidentified monacanthid		20	1.1	0.3
Mullidae	9	49	2.8	0.6
Nomeidae	26	1	0.4	<0.1
Ostraciontidae	12			
Lactoria fornasini		85	1.4	0.5
Polymixiidae	22			
Polymixia japonica		1	0.4	0.4
Priacanthidae	19			
Priacanthus cruentatus		1	0.4	<0.1
Unidentified priacanthid		1	0.4	<0.1
Scomberesocidae	10.5			
Cololabis saira		15	1.4	1.3
Scombridae	10.5			
Auxis spp.		3	0.4	0.4
Katsuwonus pelamis		5	1.8	0.6
Thunnus alalunga		1	0.4	0.1
Unidentified scombrid		1	0.4	0.1
Tetraodontidae	13			
Lagocephalus lagocephalus		3	1.1	0.6
Unidentified tetraodontid		1	0.4	0.1
Xiphiidae	26			
Xiphias gladius		1	0.4	0.1
Unidentified fishes	7	32	11.3	1.9
SEABIRDS				
Sterna fuscata	15	2	0.7	0.7
MOLLUSCA				
Decapoda				
Ommastrephidae	2			
Symplectoteuthis spp.		14	3.2	0.9
S. oualaniensis		4	1.4	0.3
S. luminosa		2	0.4	0.1
Unidentified ommastrephid		209	23.6	10.7
Unidentified squids	5	73	11.6	1.6
UNIDENTIFIED REMAINS	14	3	1.1	0.2
UNIDENTIFIED MEAT		1	0.4	0.4

ples from many locations when we desired. Carangids were the highest ranked prey family overall, and this ranking is generally consistent at each island group and season. However, carangids ranked low during winter in the Midway Island group (perhaps due to a small sample size) and ranked fourth during spring in the Laysan Island group, where they made up 8% of the volume of prey consumed. During summer at Laysan, carangids ranked highest, comprising 42% of the volume of prey taken. Goatfishes ranked very high in the Laysan group during both seasons (spring and summer) during which adequate samples were collected. Nevertheless, in the Midway Island group, goatfishes were most important during spring but were absent in the 64 samples collected during the other 3 seasons. Flyingfishes ranked uniformly high in the Laysan group throughout the seasons sampled. In contrast, this family varied in ranking and

Table 11. Lengths and volumes of some prey items[a] of the great frigatebird. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Decapterus macrosoma	3		147		160		153		4	
Pervagor spilosoma	22		42		71		60		1	
Parexocoetus brachypterus	11		129		141		135		1	
Exocoetus volitans	20	1	107	54	165	54	141	54	4	
Lactoria fornasini	42		12		22		17		<0.5	
MOLLUSCA										
Ommastrephidae	103	1	42	25	118	25	78	25	2	
Symplectoteuthis spp.	9		64		105		85		5	

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

percentage total volume in the Midway group, being first during winter (36%) and summer (53%) but fourth during spring (13%) and fall (10%). Ommastrephid squids ranked high only during spring and summer. Needlefishes (fall) and rudderfish (winter) ranked high at Midway. This analysis demonstrates that overall patterns are relatively constant, but some subtle changes in diet take place.

The diet of brown boobies in Hawaii is distinguished from diets elsewhere in the prevalence of *Decapterus* spp. and goatfishes. The brown booby apparently changes its diet greatly with location. Murphy (1936:859) mentioned the consumption of flatfishes, parrot fishes, and large prawns. Serventy (1952) listed *Rastrelliger kanagurta*, *Trachurus*, and *Chorinemus lysan* as prey in the Sahul Shelf, Australia. Dorward (1963*a*) stated it fed on blennies at Ascension Island. However, most authors have found flyingfishes to be an important component of the diet.

Red-footed Booby.—We collected and analyzed 369 samples from red-footed boobies from 1978–80. Most were taken from Midway, Laysan, and French Frigate Shoals, but some were collected on each island in the study area with the exception of Pearl and Hermes Reef. Samples came from all months except December and included adults (79%), subadults (1%), and nestlings (20%). They averaged 73 ml and 5.8 prey items. The condition of the samples was reasonably good, and more than 97% of the fishes were identified at least to family.

Fish accounted for more than 72% of the sample volumes with squid representing most of the remaining 27%. Twenty-seven fish families, 1 squid family, a copepod, and an insect were found. Pooling all years, areas, and seasons, flyingfishes ranked highest among the prey. Most of these fishes could not be identified further, but of those identified, *E. volitans*, *P. brachypterus*, and *Cypselurus* spp. were common (Table 14). Ommastrephid squids ranked second and included *Ommastrephes* spp., *Hyaloteuthis pelagicus*, *S. oualaniensis*, and *S. luminosa*. Carangidae ranked third and consisted mostly of *Decapterus* spp., especially *D. macrosoma* and *D. tabl*. Unidentified squids ranked fourth, followed by juvenile goatfishes and Pacific sauries (Table 14).

We obtained 550 measurements of prey items with a mean length of 88 mm and ranging from a 32-mm balloon fish to a 282-mm halfbeak. These data show that red-footed boobies take prey with mean lengths 50–150 mm, including *Decapterus* spp. (149 mm), *E. volitans* (126 mm), and *S. oualaniensis* (82 mm) (Table 15). The red-footed booby had fairly wide flexibility in the size of prey it consumed. We had only 41 prey items in good enough condition to be measured volumetrically.

Table 12. Prey items identified to lowest taxon in 244 brown booby samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Ammodytidae	13			
Bleekeria gillii		20	1.2	0.3
Atherinidae	15			
Pranesus insularum		12	0.4	0.3
Belonidae	6			
Platybelone argalus platyura		50	8.2	4.4
Ablennes hians		4	1.6	0.1
Blenniidae	14	5	0.4	0.4
Carangidae	1			
Decapterus spp.		145	23.8	13.8
D. macarellus		8	1.6	0.5
D. macrosoma		99	11.9	7.2
D. tabl		16	4.5	1.3
Selar crumenophthalmus		5	0.8	0.5
Naucrates ductor		14	0.2	0.2
Seriola spp.		53	8.2	3.5
Caranx spp.		9	0.8	0.1
Unidentified carangid		13	2.0	0.1
Coryphaenidae	12			
Coryphaena spp.		2	0.4	0.2
C. hippurus		3	0.8	<0.1
C. equiselis		8	1.6	0.5
Echeneidae	18.5			
Remoropsis brachypterus		2	0.8	0.1
Unidentified echeneid		1	0.4	<0.1
Exocoetidae	2.5			
Parexocoetus brachypterus		22	2.9	1.9
Exocoetus sp.		1	0.4	0.4
E. volitans		56	9.4	4.9
Prognichthys gilberti		8	0.8	0.5
Cypselurus spp.		24	7.0	5.4
C. speculiger		4	1.2	0.4
C. spilonotopterus		1	0.4	0.4
C. atrisignis		5	0.8	0.4
Unidentified exocoetid		104	24.2	11.5
Gempylidae	17			
Gempylus serpens		3	1.2	<0.1
Unidentified gempylid		1	0.4	0.1
Hemiramphidae	4			
Euleptorhamphus viridis		53	13.1	7.5
Hyporhamphus acutus pacificus		2	0.4	0.1
Oxyporhamphus micropterus		1	0.4	0.2
Unidentified hemiramphid		35	4.5	1.9
Kyphosidae	7			
Kyphosus bigibbus		68	9.0	3.6
Labridae	16			
Hemipteronotus leclusei		4	0.4	0.4
Mullidae	2.5	1,852	30.0	15.3
Nomeidae	11			
Nomeus gronovii		3	1.2	0.1
Psenes cyanophrys		11	2.0	0.6
Unidentified nomeid		9	1.6	0.1
Priacanthidae	20			
Priacanthus sp.		1	0.4	0.1
Unidentified priacanthid		2	0.4	0.1
Scomberesocidae	18.5			
Cololabis saira		4	0.4	0.3
Scombridae	10			
Scomber japonicus		2	0.8	0.7
Katsuwonus pelamis		8	2.9	1.4
Acanthocybium solandri		3	0.8	0.4
Unidentified scombrid		1	0.4	0.1
Sphyraenidae	21			
Sphyraena helleri		1	0.4	0.2
Unidentified fishes	8	46	17.6	2.3
MOLLUSCA				
Decapoda				
Ommastrephidae	5			
Ommastrephes spp.		3	0.8	0.3
Symplectoteuthis spp.		2	0.8	0.1
S. oualaniensis		1	0.4	0.1
S. luminosa		1	0.4	0.1
Unidentified ommastrephid		61	12.7	3.7
Unidentified squids	9	35	6.1	0.5
CRUSTACEA				
Isopoda	22	1	0.4	0.1

These items ranged from 0.6 to 129 ml, averaging 26 ml.

Sampling was generally adequate to compare the most common prey items for all seasons in all of the island groups of the NWHI. Flyingfishes ranked first or second in almost all seasons for all regions. Ommastrephid squids also ranked high in each season and area sampled, but were apparently most important in the French Frigate Shoals region. Carangids ranked highest during summer but were present in the species lists for most areas throughout the year. Goatfishes were present at low levels throughout the year but ranked highest in the diet of the red-footed booby during spring. Several fishes were common only during a single season. At Midway, Pacific sauries ranked second in winter and anchovies ranked third in fall. Neither occurred elsewhere during any season, nor was found in the diet of this booby during other seasons at Midway. Skipjack tunas ranked high only in fall at Midway and French Frigate Shoals. Snake

Table 13. Lengths and volumes of some prey items[a] of the brown booby. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Seriola spp.	27	5	49	6	165	41	100	31	6	6
Decapterus spp.	19	3	63	4	215	24	146.3	11	12	6
D. macrosoma	12	1	110	67	200	67	158	67	7	
Mullidae	164	2	37	2	83	2	54	2	<0.5	0
Exocoetidae	11		31		219		115		17	
Parexocoetus brachypterus	15	1	129	27	146	27	137	27	1	
Exocoetus volitans	32		107		179		128		3	
Cypselurus spp.	11		117		234		166		12	
Euleptorhamphus viridis	9		191		319		281		13	
Kyphosus bigibbus	24	1	41	9	170	9	72	9	6	
Psenes cyanophrys	8		51		128		81		10	
Cololabis saira	3		218		233		223		5	
Platybelone argalus platyura	5		205		248		231		8	
MOLLUSCA										
Ommastrephidae	48	6	41	2	129	50	81	37	4	7

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

mackerels ranked fourth at Laysan during winter. These changes in relative abundance of dietary components implies some differences of availability within a fairly constant framework.

Our results correspond generally with previous studies that indicate the prevalence of flyingfishes and ommastrephid squids in the diet of this species at Oahu, Hawaii (Ashmole and Ashmole 1967*a*), South America (Murphy 1936:869), Aldabra Atoll (Diamond 1974*b*), and Christmas Island (Pacific) (Schreiber and Hensley 1976). The diet of Hawaiian birds is unique because carangids, goatfishes, and Pacific sauries are common components.

Red-tailed Tropicbird.—We collected and analyzed 270 samples from red-tailed tropicbirds. Most were taken from French Frigate Shoals, Laysan, and Midway, with others coming from Lisianski, Nihoa, and Kure. By pooling all samples together from 1978–80, samples representing each month except January were collected. Samples were taken from adults (28%), subadults (12%), and chicks (60%). They contained an average of 57 ml and 4 prey items. The condition of the samples was fairly good, allowing for identification to family of more than 90% of the fishes.

The prey of this species consisted of 24 fish families, 2 squid families, stomatopods, and shrimps (Table 16). Prey items were 82% fish and 18% squid by volume, and a few crustaceans. Flyingfishes were the most prominent prey. Seventy-eight percent of these could not be identified further, but *E. volitans* and *Cypselurus* spp. were common among those identified. Ommastrephid squids ranked second and were primarily *S. oualaniensis*, *Ommastrephes* spp., and *Hyaloteuthis pelagicus*. The third ranked prey were the carangids, mostly *Decapterus macrosoma*. Ranking fourth and fifth were unidentified squids and dolphin-fishes, respectively (Fig. 9). The latter were *Coryphaena* and included more *C. equiselis* than *C. hippurus*. Other common prey items were truncated sunfish and balloonfish.

We obtained 169 prey items that were in good enough condition to measure. Their mean length was 101 mm and ranged from a 10-mm stomatopod to a 237-mm balloonfish. *Decapterus* spp. had a mean length of 168 mm and squids ranged 70–90 mm (Table 17). One flyingfish was only 13 mm.

The distribution of our sampling effort limits comparisons we can make among island groups and among seasons because most samples were collected during spring

Table 14. Prey items identified to lowest taxon in 360 red-footed booby samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Ammodytidae	12			
Bleekeria gillii		59	3.3	0.3
Belonidae	24			
Ablennes hians		1	0.3	0.2
Carangidae	3			
Decapterus spp.		124	13.9	6.5
D. macarellus		1	0.3	0.3
D. macrosoma		67	5.0	2.6
D. tabl		32	2.2	0.8
Seriola sp.		1	0.3	0.1
Unidentified carangid		6	0.8	0.1
Cheilodactylidae	30			
Cheilodactylus vittatus		1	0.3	<0.1
Coryphaenidae	14.5			
Coryphaena spp.		2	0.6	<0.1
C. hippurus		3	0.8	0.1
C. equiselis		3	0.6	<0.1
Diodontidae	30	1	0.3	<0.1
Engraulidae	10			
Stolephorus buccaneeri		131	2.8	0.7
Exocoetidae	1			
Parexocoetus brachypterus		22	3.3	2.3
Exocoetus volitans		59	9.4	4.7
Cypselurus spp.		48	10.0	7.1
C. speculiger		7	1.7	1.1
C. atrisignis		1	0.3	0.1
C. spilopterus		4	1.1	0.7
Unidentified exocoetid		319	50.3	29.4
Gempylidae	11			
Gempylus serpens		32	5.8	0.5
Unidentified gempylid		1	0.3	<0.1
Gonorhynchidae	18			
Gonorhynchus gonorhynchus		7	0.6	0.1
Gonostomatidae	16			
Vinciguerria spp.		2	0.3	<0.1
V. nimbaria		33	0.3	0.1
Hemiramphidae	9			
Euleptorhamphus viridis		11	3.1	1.1
Oxyporhamphus micropterus		10	1.7	0.8
Unidentified hemiramphid		2	0.6	0.2
Holocentridae	22.5			
Sargocentron sp.		1	0.3	<0.1
Unidentified holocentrid		1	0.3	<0.1
Istiophoridae	22.5	2	0.6	<0.1
Kyphosidae	25.5			
Kyphosus bigibbus		2	0.3	<0.1
Macrorhamphosidae	30			
Macrorhamphosus gracilis		1	0.3	<0.1
Molidae	13			
Ranzania laevis		18	3.1	1.7
Masturus lanceolatus		2	0.3	0.1
Monacanthidae	19	4	0.6	0.1
Mullidae	6	156	8.9	1.6
Myctophidae	30	1	0.3	<0.1
Nomeidae	14.5			
Psenes cyanophrys		4	0.3	0.1
Unidentified nomeid		10	1.1	0.1
Priacanthidae	20	2	0.6	0.1
Scomberesocidae	5			
Cololabis saira		59	6.4	4.3
Scombridae	8			
Katsuwonus pelamis		19	4.4	2.5
Thunnus sp.		1	0.3	0.3
Unidentified scombrid		3	0.8	0.3
Sphyraenidae	30	1	0.3	<0.1
Synodontidae	21	3	0.8	<0.1
Tetraodontidae	30			
Lagocephalus lagocephalus		1	0.3	<0.1
Unidentified fishes	7	39	10.6	1.4
MOLLUSCA				
Decapoda				
Ommastrephidae	2			
Ommastrephes spp.		9	0.8	0.3
Symplectoteuthis spp.		41	8.3	1.9
S. oualaniensis		57	7.2	3.2
S. luminosa		11	0.8	0.5
Hyaloteuthis pelagicus		16	1.9	0.3
Unidentified ommastrephid		508	37.5	19.0
Unidentified squids	4	130	14.2	2.0
CRUSTACEA				
Copepoda	25.5			
Pennellidae				
Penella spp.		2	0.3	<0.1
INSECTA	30	1	0.3	<0.1
UNIDENTIFIED REMAINS	17	3	0.8	0.2

or summer. Flyingfishes ranked highest at most locations for all seasons in which sampling was possible. Ommastrephid squids also ranked high throughout the year but were apparently more so during spring than during summer. *Decapterus* spp. were common during summer but not during winter or spring. Dolphin-fishes were sporadically common throughout the sampling period at various locations. Two fishes were taken only seasonally. Pacific sauries ranked high during winter in the Midway region but did not occur elsewhere. Truncated sun fish occurred only during summer and did not rank high anywhere except French Frigate Shoals. Red-tailed tropicbirds fed heavily on 130–

Table 15. Lengths and volumes of some prey items[a] of the red-footed booby. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Decapterus tabl	8		62		177		97		16	
Decapterus spp.	9		83		214		149		13	
D. macrosoma	4		147		173		163		5	
Stolephorus buccaneeri	45		57		83		69		1	
Oxyporhamphus micropterus	8	5	111	12	180	38	141	25	8	5
Parexocoetus brachypterus	10	3	113	19	142	33	131	27	3	4
Exocoetus volitans	36	3	76	16	208	26	126	21	5	3
Mullidae	3		54		60		58		2	
MOLLUSCA										
Ommastrephidae	256	17	40	6	208	43	78	24	1	2
Symplectoteuthis spp.	32	1	38	13	117	13	70	13	3	
S. oualaniensis	45	3	54	12	131	26	82	21	2	5
Hyaloteuthis pelagicus	14		49		110		60		4	

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

160 mm flyingfishes and *Decapterus* spp. and 70–90 mm ommastrephid squids.

Flyingfishes (especially *Cypselurus* spp. and *E. volitans*) and squids are known to occur in the diet of this species at Christmas Island (Indian) (Gibson-Hill 1947), Kure (Fleet 1974), Christmas Island (Pacific) (Ashmole and Ashmole 1967*b*), and Aldabra Atoll (Diamond 1975). The diet of this species in Hawaii is unique in the prevalence of carangids, dolphin-fishes, and sun fish.

Wedge-tailed Shearwater.—During 1978–80, we collected 233 samples from wedge-tailed shearwaters. Collections were possible only May–November. This species does not visit its colonies between breeding seasons, and courting adults that come to shore in early spring apparently live off fat reserves and have empty stomachs. Most of our samples were taken from Oahu, Laysan, and Midway, but some were taken from each island in our study area except Necker and Lisianski. Many of the samples were in fairly advanced states of digestion. For this reason 80% of the samples were taken from adults and 20% from dependent young because adults had less-digested samples. Samples displaced an average 16 ml and contained 8.4 prey items. More than 96% of the fishes could be identified to family, and 51% could be identified to genus or species.

We found 21 fish families, a squid family, an octopus, a stomatopod, an isopod, a crab, an insect, and a coelenterate (Table 18). By volume, the prey constituted 66% fish, 28% squid, and 1% crustaceans. As with all procellariiformes, stomach oil was regurgitated, but we ignored this component in our laboratory analysis. Pooling all months, years, and locations, the highest ranked prey was goatfishes (Fig. 10). No attempt was made to further identify this family because samples were comprised of juveniles, many of which were very well-digested. The second ranked prey item was Carangidae, including *Decapterus macrosoma*, *D. tabl*, and probably *D. macarellus* and *D. muroadsi*. The third and fourth ranked prey items were Ommastrephidae (including *S. oualaniensis*) and unidentified squids. It is likely that most of the unidentified squids were ommastrephids. Other common prey items included filefish, flyingfishes, and gobies.

The lengths of the 212 prey items that were in good enough condition for reliable measurement averaged 57 mm, rang-

Table 16. Prey items identified to lowest taxon in 270 red-tailed tropicbird samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Ammodytidae	29			
Bleekeria gillii		1	0.4	0.1
Belonidae	19			
Ablennes hians		1	0.4	0.1
Unidentified belonid		1	0.4	0.2
Carangidae	3			
Decapterus spp.		53	15.9	9.5
D. macrosoma		29	4.8	3.6
D. tabl		1	0.4	0.1
Naucrates ductor		1	0.4	0.4
Coryphaenidae	5			
Coryphaena spp.		13	4.8	2.9
C. hippurus		9	3.3	2.4
C. equiselis		18	6.7	3.9
Diodontidae	14			
Diodon spp.		3	1.1	0.3
D. hystrix		1	0.4	0.1
Unidentified diodontid		2	0.7	0.2
Echeneidae	21			
Remoropsis brachypterus		1	0.4	0.1
Unidentified echeneid		1	0.4	0.1
Exocoetidae	1			
Parexocoetus brachypterus		3	0.7	0.5
Exocoetus volitans		22	7.4	3.2
Cypselurus spp.		20	5.9	3.4
C. speculiger		1	0.4	0.3
C. spilopterus		1	0.4	0.4
Unidentified exocoetid		167	39.6	24.1
Gempylidae	13			
Gempylus serpens		8	3.0	0.3
Unidentified gempylid		1	0.4	<0.1
Hemiramphidae	11			
Euleptorhamphus viridis		10	2.6	1.6
Unidentified hemiramphid		5	1.5	0.4
Istiophoridae	22	1	0.4	0.4
Kyphosidae	15.5			
Kyphosus bigibbus		4	1.1	0.6
Molidae	7			
Ranzania laevis		23	5.2	4.3
Masturus lanceolatus		2	0.7	0.5
Monacanthidae	23	2	0.4	0.1
Mullidae	17	5	1.5	0.3
Myctophidae	29	1	0.4	<0.1
Nomeidae	15.5			
Cubiceps pauciradiatus		1	0.4	0.1
Unidentified nomeid		4	1.5	0.2
Pomacentridae	25.5	1	0.4	0.1
Priacanthidae	29			
Priacanthus sp.		1	0.4	<0.1
Scomberesocidae	9			
Cololabis saira		18	4.1	4.1
Scombridae	16			
Auxis spp.		2	0.7	0.5
Katsuwonus pelamis		7	2.6	2.2
Unidentified scombrid		3	1.1	0.7
Synodontidae	20	11	0.4	0.1
Tetraodontidae	8			
Lagocephalus lagocephalus		13	4.8	3.2
Unidentified tetraodontid		4	1.1	0.6
Xiphiidae	12			
Xiphias gladius		7	2.6	1.5
Tetrodontoidei (puffer)	25.5	1	0.4	0.1
Unidentified fishes	6	50	16.7	4.0
MOLLUSCA				
Decapoda				
Ommastrephidae	2			
Ommastrephes sp.		1	0.4	<0.1
Symplectoteuthis spp.		20	6.3	2.2
S. oualaniensis		16	4.8	2.4
Hyaloteuthis pelagicus		1	0.4	0.1
Unidentified ommastrephid		139	24.4	10.1
Onychoteuthidae	18			
Onychoteuthis spp.		2	0.4	0.4
Unidentified onychoteuthid		1	0.4	<0.1
Unidentified squids	4	354	17.4	2.6
CRUSTACEA				
Stomatopoda	24			
Lysiosquilla spp.		2	0.4	<0.1
Unidentified stomatopod		1	0.4	<0.1
Shrimp	29	1	0.4	<0.1
UNIDENTIFIED REMAINS	29	1	0.4	<0.1

ing from a 4-mm sea-strider to a 145-mm *D. macrosoma* (Table 19). Juvenile goatfishes had a mean length of 54 mm, and ommastrephid squids had a mean length of 63 mm. Unfortunately, we only had a few *Decapterus* spp. measurements, but those we had were in the 80–100 mm range.

Our inability to collect samples from several places in the archipelago during some seasons precludes a detailed analysis of changes in diet with season and island group. It is apparent that goatfishes ranked highest during spring and continued to rank high in the Laysan region but not Midway during summer. Ommastrephid squids ranked high in the Midway region throughout the 3 seasons sampled and ranked first at Oahu during fall. These

Fig. 9. Dolphin-fish, a prey item.

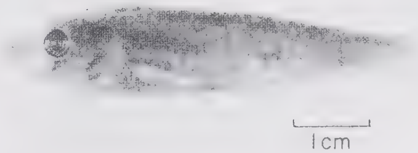

Fig. 10. Goatfish, a prey item.

squids also ranked high in the Laysan region during spring but less so during summer. Carangids ranked higher in the Laysan Island group than Midway, especially during summer when they constituted 60% by volume at Laysan, but they did not occur in any of the 12 samples from Midway. Lanternfishes ranked high only during spring at Midway, and filefishes were important only in the Laysan Island group. Wedge-tailed shearwaters fed heavily on ommastrephid squids during fall but supplemented this food source with prey items that were not taken during spring or summer. These included anchovies, crabs, and stomatopods in the Midway region and gobies in the Oahu region, neither of which were taken anywhere during spring or summer. This species fed heavily on goatfishes, *Decapterus* spp., and ommastrephid squids in the 50–100 mm size class and took other prey items when available. Fragmentary information from the Indian Ocean (Bailey and Bourne 1963) indicates that squids are consumed by this species elsewhere.

Christmas Shearwater.—During 1978–80 we collected and analyzed 182 samples from Christmas shearwaters. Most came from Laysan, but some were collected on each island in the Hawaiian Archipelago with the exceptions of Necker and Oahu. Because this species does not make landfall when it is not breeding, our sampling was restricted to March–September. Although a few samples were taken from nestlings (4%), most (96%) were taken from adults. The samples had a mean volume of 15 ml and contained a mean of 5.4 prey items. This is half the number of prey items per sample found by Ashmole and Ashmole (1967*b*). Despite the fairly digested condition of many of the sam-

Table 17. Lengths and volumes of some prey items[a] of the red-tailed tropicbird. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Decapterus spp.	6		140		216		168		13	
D. macrosoma	5	1	131	65	181	65	153	65	8	
Coryphaena hippurus	3	2	111	12	189	78	148	45	23	33
C. equiselis	4		134		183		163		11	
Exocoetidae	11		13		201		133		14	
Exocoetus volitans	16	2	124	36	159	46	140	41	3	5
Ranzania laevis	5	1	123	34	140	34	130	34	4	
MOLLUSCA										
Ommastrephidae	58		23		128		82		3	
Symplectoteuthis spp.	10		52		120		80		6	
S. oualaniensis	14	1	60	32	113	32	90	32	4	

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods)

Table 18. Prey items identified to lowest taxon in 233 wedge-tailed shearwater samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Ammodytidae	30.5			
Bleekeria gillii		1	0.4	<0.1
Carangidae	2			
Decapterus spp.		64	13.3	8.5
D. macrosoma		55	14.6	11.5
D. tabl		19	6.4	4.7
Selar crumenophthalmus		4	0.9	0.2
Seriola sp.		1	0.4	0.2
Unidentified carangid		2	0.9	0.1
Clupeidae	15			
Sardinella marquesensis		7	0.9	0.5
Coryphaenidae	17			
Coryphaena sp.		1	0.4	<0.1
C. equiselis		3	1.3	0.2
Dactylopteridae	30.5			
Dactyloptena orientalis		1	0.4	<0.1
Engraulidae	14			
Stolephorus buccaneeri		8	0.9	0.8
Exocoetidae	8.5			
Parexocoetus brachypterus		1	0.4	0.4
Unidentified exocoetid		22	7.7	3.4
Fistulariidae	30.5	1	0.4	<0.1
Gempylidae	19.5			
Gempylus serpens		4	1.3	0.1
Gobiidae	7			
Ptereleotris heteropterus		517	2.6	1.4
Gonostomatidae	13			
Vinciguerria spp.		38	0.9	0.4
Holocentridae	17	6	2.1	0.1
Kyphosidae	30.5			
Kyphosus bigibbus		1	0.4	<0.1
Monacanthidae	6			
Pervagor spilosoma		13	0.9	0.7
Unidentified monocanthid		33	6.9	3.0
Mullidae	1	521	31.8	17.6
Myctophidae	8.5	28	4.7	3.8
Nomeidae	10			
Psenes sp.		1	0.4	0.1
Unidentified nomeid		24	3.9	1.5
Priacanthidae	27	1	0.4	0.4
Scombridae	17			
Katsuwonus pelamis		4	1.7	0.2
Synodontidae	22	4	0.9	0.1
Tetraodontidae	25.5	2	0.9	0.1
Leptocephalus larvae	30.5	1	0.4	<0.1
Unidentified fishes	5	53	15.0	5.8
MOLLUSCA				
Decapoda				
Ommastrephidae	3			
Symplectoteuthis spp.		21	6.4	4.0
S. oualaniensis		9	3.0	2.5
Hyaloteuthis pelagicus		1	0.4	0.3
Unidentified ommastrephid		138	25.8	15.0
Unidentified squids	4	281	21.5	6.4
Octopoda	24	2	0.4	0.4
CRUSTACEA				
Stomatopoda	23			
Lysiosquilla spp		5	0.4	0.2
Parasitic isopod	25.5	2	0.9	0.1
Crab	19.5			
Brachyura		1	0.4	<0.1
Crab megalopa		19	0.4	0.2
Unidentified crustacean	12	24	1.3	0.6
INSECTA				
Gerridae	21			
Halobates sericeus		3	1.3	0.1
COELENTERATA				
Scyphozoa	30.5	1	0.4	<0.1
UNIDENTIFIED REMAINS	11	15	6.4	3.2

ples, 95% of the fishes could be identified at least to family.

Prey items came from 17 fish families, 2 squid families, and a crustacean. Ignoring the stomach oil component of the samples, we found the prey to be 50% fish and 48% squid by volume. The highest ranking prey item was Ommastrephidae (Table 20), including *S. oualaniensis* and *H. pelagicus*. Ranking next were goatfishes. Flyingfishes ranked third and although few were identified, *E. volitans* was present. The fourth ranking family was Carangidae, consisting entirely of the genus *Decapterus*, and included *D. macrosoma*. Other common prey families included squirrelfishes and rudderfish (Table 20).

We obtained 198 measureable prey items. The mean prey length was 65 mm, ranging from a 25-mm squid to a 134-mm *D. macrosoma*. Most measurements were squids, with a mean length of 62 mm for Ommastrephidae (Table 21). Average lengths for commonly consumed fishes ranged from 53 mm (goatfishes) to 126 mm (*Decapterus* spp.).

Table 19. Lengths and volumes of some prey items[a] of the wedge-tailed shearwater. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Mullidae	41		48		64		54		1	
Ptereleotris heteropterus	30	20	22	0.2	30	0.2	28	0.2	<0.5	0
Myctophidae	14		14		80		71		5	
MOLLUSCA										
Ommastrephidae	69		29		115		63		3	
Symplectoteuthis spp.	21		39		112		67		4	
S. oualaniensis	9		57		100		85		5	

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

Sampling was adequate to discuss seasonal changes only for the Laysan region. It is apparent that Ommastrephidae was the highest ranked prey item in the diet of the Christmas shearwater in virtually all island groups and seasons sampled. Goatfishes ranked high during winter, spring, and summer on Laysan. They comprised much more of the prey volume during spring (30%) than summer (6%). In contrast, flyingfishes were ranked highest there during summer, climbing from 1% by volume in spring to 21% in summer. The limited sampling in the Midway and French Frigate Shoals regions indicated flyingfishes were eaten whenever samples were obtained. Carangids were not present in the Midway samples, but this may have been due to insufficient sampling. In the Laysan region, where sampling was sufficient, carangids were more important by volume in summer (25%) than spring (5%). Lizardfishes ranked second in the Laysan area during winter, and rudderfish ranked first during summer in the Midway region. Christmas shearwaters exploited many food sources but fed most heavily on ommastrephid squids, goatfishes, flyingfishes, and *Decapterus* spp. in the 50–100 mm range.

Hawaiian birds consumed less squid (48% vs. 71%, by volume) than shearwaters on Christmas Island (Ashmole and Ashmole 1967*b*). In addition, Hawaiian birds ate many goatfishes and carangids whereas Christmas Island birds consumed many tunas and bristlemouths. Birds at both locations commonly took flyingfishes.

Brown Noddy.—We collected and analyzed 354 samples from brown noddies, most coming from Pearl and Hermes Reef, Lisianski, Laysan, and French Frigate Shoals. Some samples were obtained from each island in the archipelago. Samples were collected March–November with many more (84%) coming from adults than subadults (5%) or nestlings (11%). Pooling all samples collected 1978–80, the mean volume was 14 ml and contained an average 7.7 prey items/sample. Sample condition was relatively good, enabling 97% of the fishes to be identified to family.

The sample volumes contained 66% fish and 33% squid. Thirty-three fish families, 2 squid families, 2 crustacean groups, and a marine insect were found (Table 22). The highest ranking prey was juvenile goatfishes. Ommastrephid squids ranked next and included *S. oualaniensis, S. luminosa*, and *Ommastrephes* spp. Juvenile lizardfishes ranked third. Carangids, most of which were *Decapterus* spp., ranked fourth. Other common prey families were flyingfishes (especially *E. volitans*) and snake mackerels.

We found 460 measureable prey items. They averaged 48 mm and ranged from a 3-mm sea-strider to a 185-mm *Decapterus* sp. Goatfishes and ommastrephid squids had mean lengths of 58 and 53 mm,

Table 20. Prey items identified to lowest taxon in 182 Christmas shearwater samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Ammodytidae	14			
Bleekeria gillii		10	3.8	0.4
Carangidae	4			
Decapterus spp.		57	15.4	10.6
D. macrosoma		6	2.7	1.8
Unidentified carangid		2	0.5	0.5
Coryphaenidae	19			
Coryphaena hippurus		1	0.5	<0.1
C. equiselis		1	0.5	0.1
Dactylopteridae	22			
Dactyloptena orientalis		2	1.1	<0.1
Exocoetidae	3			
Exocoetus volitans		1	0.5	0.2
Unidentified exocoetid		81	26.4	9.6
Gempylidae	12			
Gempylus serpens		8	4.4	0.9
Gonorhynchidae	16			
Gonorhynchus gonorhynchus		5	2.7	0.2
Gonostomatidae	11			
Vinciguerria spp.		39	2.2	1.4
Hemiramphidae	20			
Oxyporhamphus micropterus		1	0.5	0.5
Holocentridae	7	25	7.1	2.3
Istiophoridae	24	1	0.5	0.1
Macrorhamphosidae	15			
Macrorhamphosus gracilis		5	1.6	0.5
Monacanthidae	21	2	0.5	0.2
Mullidae	2	256	35.2	14.2
Nomeidae	8	22	4.4	2.4
Scombridae	13			
Katsuwonus pelamis		6	2.7	0.8
Sternoptychidae	17	3	1.1	0.2
Synodontidae	9	28	4.9	0.7
Unidentified fishes	6	31	14.8	2.3
MOLLUSCA				
Decapoda				
Ommastrephidae	1			
Symplectoteuthis spp.		42	12.6	7.0
S. oualaniensis		7	3.3	1.5
Hyaloteuthis pelagicus		12	3.8	2.0
Unidentified ommastrephid		260	47.8	31.7
Onychoteuthidae	18	2	0.5	0.5
Unidentified squids	5	58	20.3	5.3
CRUSTACEA				
Crustacean larvae	23	4	0.5	<0.1
UNIDENTIFIED REMAINS	10	10	4.4	1.7

respectively. Juvenile lizardfishes averaged 40 mm (Table 23). Most prey taken by brown noddies was 20–80 mm.

Although sampling was somewhat inadequate during fall and winter, some interesting patterns emerge from a comparison of the 4 island groups and 4 seasons. Goatfishes ranked highest throughout the Hawaiian Archipelago in spring, but declined in summer, especially in the 2 northern island groups. They remained fairly common during fall and winter but much less so compared to spring and summer. Ommastrephid squids ranked higher than goatfishes during fall and winter, ranking first in both areas sampled. They ranked second in most island groups during spring and summer and were consequently a very common prey item throughout the year. Lizardfishes ranked highest of the fish prey during winter. They also ranked high during spring but declined considerably during summer when other prey resources were eaten. During summer and fall, goatfishes occurred in only 1 of 36 samples at Midway. *Decapterus* spp. did not occur in any of 15 fall or 40 winter samples, yet ranked high during spring and very high during summer, especially in the Laysan Island group. Flyingfishes were highly ranked only in summer, especially in the Midway Island group where many *E. volitans* were taken. A few flyingfishes were taken during winter and spring. Many were taken on Midway during October. Dorward and Ashmole (1963:453) found that brown noddies took few *E. volitans* on Ascension Island, even though other seabirds obtained it. Snake mackerels were regularly taken in all island groups during all seasons, whereas squirrelfishes were most important only during summer at the northern end of the archipelago. Anchovies occurred only during fall at Midway, ranking second there. These results display intriguing changes in diet with season, presumably due to changes in prey availability in surface waters.

The diet of the brown noddy is different in Hawaii than at other locations. We found many goatfishes, ommastrephid squids, flyingfishes, and carangids as did Brown (1975) at Oahu. Dorward and Ashmole (1963) found blennies, halfbeaks, flyingfishes, and squirrelfishes but few

Table 21. Lengths and volumes of some prey items[a] of the Christmas shearwater. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Decapterus spp.	4		120		131		126		3	
Mullidae	7		51		57		53		1	
Exocoetidae	15		38		125		80		6	
MOLLUSCA										
Ommastrephidae	109		25		107		62		2	
Symplectoteuthis spp.	39	4	30	1	99	17	61	7	3	4
S. oualaniensis	7	1	74	12	94	12	84	11	3	
Hyaloteuthis pelagicus	10		53		64		58		1	

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

squids at Ascension Island. At Christmas Island (Pacific), most fishes were flyingfishes, tunas, and snake mackerels (Ashmole and Ashmole 1967*b*).

Sooty Tern.—We collected 356 samples from sooty terns, obtaining some from each island group in the Hawaiian Archipelago. Most came from Laysan, Lisianski, and French Frigate Shoals. Because this species does not make landfall when not breeding, collecting was restricted to March–September. We took samples from adults (68%), subadults (8%), and nestlings (24%). Pooling all samples from 1978–80, the mean sample volume was 10.4 ml, and a sample contained an average 4.5 prey items. Sample condition was reasonably good with 97% of the fishes identified to family.

Sample volumes were 46% fish and 53% squid, a separation almost identical to that reported by Brown (1975). Twenty-six fish families, 1 squid family, 1 shrimp, and 2 coelenterate groups were identified (Table 24). Squids were clearly the highest ranked prey items, with ommastrephid squids ranking first and the unidentified ones ranking third. Most of those identified were *Symplectoteuthis* spp., including *S. oualaniensis*. *Ommastrephes* spp. and *H. pelagicus* were also present. Goatfishes ranked highest among fish families. Next were flyingfishes, especially *Cypselurus* spp. and *E. volitans*. Other highly ranked prey included snake mackerels, carangids (especially *Decapterus* spp.), nomeids, and squirrelfishes.

Reliable length measurements were taken of 326 prey items. They ranged from a 1-mm gastropod to a 120-mm needlefish and averaged 48 mm. All of the common prey items for which adequate measurements were available were 20–70 mm (Table 25). The smallest of the highly ranked prey, the squirrelfishes, averaged 25 mm whereas the largest, *Exocoetus volitans*, averaged 71 mm. A few of the prey items were in good enough condition for reliable volumetric measurements. Ommastrephid squids and *E. volitans* had average volumes of 5 and 6 ml, respectively (Table 25).

Although we could not obtain samples from sooty terns during fall, some interesting patterns of seasonal and geographical variation in diet are evident. Squids were commonly eaten in all island groups, ranking either first or second in winter, spring, and summer. If the unidentified squids, which are probably Ommastrephidae, were to be added to those that were definitely from this family, the importance of ommastrephid squids in the diet would be further underscored. Goatfishes were most prominent during spring and were also commonly eaten during winter and summer. Flyingfishes were eaten seasonally. They did not occur in any of the 33 samples collected during winter, occurred in only a few of the sam-

Table 22. Prey items identified to lowest taxon in 354 brown noddy samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Ammodytidae	19			
Bleekeria gillii		10	2.0	0.2
Blenniidae	15.5	20	2.8	0.1
Bothidae	39	1	0.3	<0.1
Bramidae	39			
Pteraclis velifer		1	0.3	<0.1
Carangidae	4			
Decapterus spp.		68	11.6	6.5
D. macrosoma		24	2.5	1.8
D. tabl		11	2.0	0.9
Selar crumenophthalmus		7	1.4	0.8
Naucrates ductor		1	0.3	<0.1
Seriola sp.		1	0.3	<0.1
Unidentified carangid		6	0.8	<0.1
Chaetodontidae	39	1	0.3	<0.1
Cheilodactylidae	26.5			
Cheilodactylus vittatus		4	0.8	0.1
Cirrhitidae	29.5			
Cirrhitops fasciatus		5	0.3	0.2
Clupeidae	11			
Spratelloides delicatulus		67	0.8	0.8
Coryphaenidae	28			
Coryphaena equiselis		2	0.6	0.3
Engraulidae	17			
Stolephorus buccaneeri		9	0.8	0.6
Exocoetidae	5			
Parexocoetus brachypterus		2	0.6	0.6
Exocoetus volitans		10	2.8	2.3
Cypselurus spp.		5	1.4	0.6
Unidentified exocoetid		59	12.4	5.4
Fistulariidae	35	2	0.3	<0.1
Gempylidae	6			
Gempylus serpens		83	12.1	2.5
Unidentified gempylid		2	0.6	0.2
Gobiidae	32			
Ptereleotris heteropterus		6	0.6	<0.1
Gonorhynchidae	13			
Gonorhynchus gonorhynchus		16	2.8	0.4
Gonostomatidae	20.5			
Vinciguerria spp.		30	0.6	0.3
Hemiramphidae	39	1	0.3	<0.1
Holocentridae	8			
Neoniphon sammara		6	0.3	0.3
Sargocentron spp.		21	2.3	0.6
Unidentified holocentrid		81	5.6	1.0
Istiophoridae	33			
Makaira nigricans		2	0.6	<0.1
Unidentified istiophorid		1	0.3	<0.1
Kyphosidae	39			
Kyphosus bigibbus		1	0.3	<0.1
Macrorhamphosidae	18			
Macrorhamphosus gracilis		10	2.3	0.2
Molidae	23			
Ranzania laevis		3	0.8	0.6
Monacanthidae	14			
Pervagor spilosoma		3	0.3	0.3
Unidentified monacanthid		10	1.1	0.7
Mullidae	1	945	48.0	28.3
Myctophidae	24	4	0.6	0.4
Nomeidae	20.5	13	0.8	0.3
Pomacentridae	31	4	0.8	<0.1
Scomberesocidae	39			
Cololabis saira		1	0.3	<0.1
Scombridae	12			
Katsuwonus pelamis		6	1.7	0.3
Thunnus alalunga		1	0.3	<0.1
Unidentified scombrid		8	1.4	0.1
Sphyraenidae	15.5			
Sphyraena helleri		1	0.3	0.3
Unidentified sphyraenid		6	1.7	0.1
Synodontidae	3	682	23.7	5.9
Tetraodontidae	26.5			
Lagocephalus lagocephalus		2	0.3	0.1
Unidentified tetraodontid		2	0.6	<0.1
Leptocephalus larvae	10	17	3.1	0.5
Unidentified fishes	9	50	12.7	1.6
MOLLUSCA				
Decapoda				
Ommastrephidae	2			
Ommastrephes spp.		4	0.6	0.3
Symplectoteuthis spp.		51	9.0	4.9
S. oualaniensis		6	1.7	1.1
S. luminosa		3	0.3	0.1
Unidentified ommastrephid		228	33.6	21.6
Onychoteuthidae	34			
Onychoteuthis sp.		1	0.3	0.1
Unidentified squids	7	58	14.1	4.8
CRUSTACEA				
Euphausiacea	25	28	0.3	0.1
Stomatopoda	29.5			
Lysiosquilla sp.		1	0.3	<0.1
Odontodactylus spp.		2	0.3	<0.1
O. brevirostris		1	0.3	<0.1
INSECTA				
Gerridae	39			
Halobates sericeus		1	0.3	<0.1
UNIDENTIFIED REMAINS	22	4	1.1	0.3

ples from spring, yet ranked first or second for 3 island groups during summer. The 8 samples collected on Oahu in summer contained no flyingfishes, but Brown (1975) found them to be common in the diet there during July and August. Snake mackerels were a common component of the diet at all island groups and seasons sampled. *Decapterus* spp. did not occur

Table 23. Lengths and volumes of some prey items[a] of the brown noddy. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Holocentridae	25	14	15	0.1	38	0.4	24	0.2	1	0
Decapterus spp.	7		21		185		93		21	
Mullidae	95	2	40	2	108	2	58	2	2	0
Monacanthidae	7		31		60		45		4	
Blenniidae	16		20		27		24		1	
Spratelloides delicatulus	37		21		47		39		1	
Synodontidae	84	6	24	0.2	55	0.4	40	0.3	1	0
MOLLUSCA										
Ommastrephidae	89	3	19	2	96	28	53	13	2	8
Symplectoteuthis spp.	30	9	27	1	72	10	47	4	2	1

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

in any of the 33 samples taken during winter but were ranked fairly high during spring and summer. Squirrelfishes ranked highest during summer at the northern end of the Hawaiian Archipelago, and 75 of the 76 individuals found in this study were collected July–September. Striped hawkfish, skipjack tuna, bristlemouths, and nomeids ranked fairly high at certain areas and seasons. Sooty terns ate ommastrephid squids throughout the year and supplemented this with seasonally available fishes from several families in the 20–70 mm size range.

Sooty terns fed heavily on ommastrephid squids and flyingfishes at Ascension Island (Ashmole 1963*b*), Christmas Island (Pacific) (Ashmole and Ashmole 1967*b*), and Oahu (Brown 1975). Squid and fish species changed with location. Goatfishes and *Decapterus* spp. were common in the diet in Hawaii but unreported elsewhere.

Bonin Petrel.—During 1979–80, we collected 144 samples from Bonin petrels. A single sample was obtained in December and the remainder March–June. All but 2 were from adults (99%) and, except for 5 samples from Midway, all came from Laysan or Lisianski. Although Bonin petrels will make landfall during almost any month, we had extreme difficulty collecting samples during months when adults were not feeding their young. Most birds handled June–January would not regurgitate, and stomachs from sacrificed birds were empty during those months. Samples were well-digested. Nevertheless, more than 74% of the individual fishes could be identified at least to family. Sample volumes averaged 5.9 ml and contained on an average 4.5 prey items.

We found 12 fish families, 3 squid families, 7 crustacean groups, 1 insect, and a tunicate in the diet of this species (Table 26). By volume, the prey consisted of 47% fish, 21% squid, 7% crustaceans, and 24% unidentified remains. The highest ranking prey categories were unidentified squids, unidentified fishes, and unidentified remains. These categories are not very useful because each may be an aggregate of many taxa. Midwater lanternfishes and hatchetfishes ranked as the most important identifiable families. Two of the lanternfishes were identified by John E. Fitch using otoliths to be *Hygophum* sp. and *Myctophum* sp., and 2 of the hatchetfishes were *Argyropelecus* spp. Juvenile goatfishes and sea-striders were also high ranking components of the diet. The most common squid family was Ommastrephidae.

We obtained only 57 reliable prey lengths, which averaged 28 mm and ranged from a 3-mm sea-strider to a 112-mm conger eel. Our best measurements

Table 24. Prey items identified to lowest taxon in 356 sooty tern samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Ammodytidae	14			
Bleekeria gillii		18	3.1	0.7
Atherinidae	28			
Pranesus insularum		1	0.3	<0.1
Belonidae	27			
Ablennes hians		1	0.3	<0.1
Blenniidae	18	10	0.8	0.1
Bramidae	23			
Pteraclis velifer		1	0.3	0.1
Carangidae	5.5			
Decapterus spp.		21	4.8	2.7
D. macrosoma		9	2.2	1.8
D. tabl		26	4.2	2.0
Naucrates ductor		2	0.6	0.2
Unidentified carangid		1	0.3	<0.1
Cheilodactylidae	21			
Cheilodactylus vittatus		2	0.6	0.2
Cirrhitidae	16	7	1.4	0.2
Clupeidae	17			
Spratelloides delicatulus		27	0.3	0.3
Coryphaenidae	28			
Coryphaena hippurus		1	0.3	<0.1
Dactylopteridae	28			
Dactyloptena orientalis		1	0.3	<0.1
Echeneidae	28	1	0.3	<0.1
Exocoetidae	4			
Exocoetus volitans		21	2.8	2.2
Cypselurus spp.		41	2.5	1.0
Unidentified exocoetid		124	14.3	5.3
Gempylidae	5.5			
Gempylus serpens		73	12.6	2.9
Unidentified gempylid		2	0.6	<0.1
Gonostomatidae	13			
Vinciguerria spp.		18	0.8	0.1
V. nimbaria		20	0.3	0.3
Hemiramphidae	20			
Oxyporhamphus micropterus		3	0.8	0.1
Holocentridae	8			
Sargocentron spp.		17	1.7	0.6
Unidentified holocentrid		59	3.9	0.9
Macrorhamphosidae	28			
Macrorhamphosus gracilis		1	0.3	<0.1
Molidae	15			
Ranzania laevis		11	2.2	1.0
Monacanthidae	11			
Pervagor spilosoma		2	0.3	0.1
Cantherhines spp.		9	1.7	0.8
C. verecundus		1	0.3	0.3
Unidentified monacanthid		9	1.7	0.6
Mullidae	2	317	31.7	14.0
Myctophidae	28	1	0.3	<0.1
Nomeidae	7			
Nomeus gronovii		1	0.3	0.2
Unidentified nomeid		49	7.3	2.8
Pomacentridae	28	1	0.3	<0.1
Scombridae	10			
Katsuwonus pelamis		28	5.3	1.6
Thunnus sp.		1	0.3	0.1
Unidentified scombrid		7	2.0	0.7
Synodontidae	12	27	3.7	0.5
Xiphiidae	22			
Xiphias gladius		2	0.6	0.1
Unidentified fishes	9	38	9.3	1.5
MOLLUSCA				
Decapoda				
Ommastrephidae	1			
Ommastrephes sp.		1	0.3	0.3
Symplectoteuthis spp.		80	13.8	8.4
S. oualaniensis		19	3.9	2.8
Hyaloteuthis pelagicus		7	1.7	0.6
Unidentified ommastrephid		294	39.6	28.6
Unidentified squids	3	113	24.4	12.7
CRUSTACEA				
Shrimp	28	1	0.3	<0.1
COELENTERATA	19			
Vellellidae				
Velella velella		4	0.6	0.1
Scyphozoa		2	0.3	<0.1

were goatfishes ($\bar{x} = 51.3$ mm) and ommastrephid squids ($\bar{x} = 46$ mm) (Table 27).

We did not collect enough samples to draw many conclusions concerning variations in diet by area or season. Squids were the highest ranked prey during both winter and spring in the Laysan Island group, and they were followed in each season by lanternfishes. Hatchetfishes were present during winter and spring in the Laysan group but only during spring at Midway. Goatfishes and sea-striders occurred only during spring in the Laysan Island group.

There have been no previous studies of the diet of the Bonin petrel. Phoenix petrels at Christmas Island fed on 78% squid (primarily Ommastrephidae), 14% fish (primarily snake mackerels), and 8% invertebrates (sea-striders) (Ashmole and Ashmole 1967*b*). Gray-faced petrels fed

Table 25. Lengths and volumes of some prey items[a] of the sooty tern. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Holocentridae	17	4	16	0.1	39	0.4	25	0.3	2	0
Mullidae	35		38		61		53		1	
Spratelloides delicatulus	11		22		45		31		2	
Exocoetus volitans	10	5	32	2	114	19	71	6	8	3
Nomeidae	10		14		78		51		8	
Cantherhines spp.	6	3	34	2	57	5	43	4	4	1
MOLLUSCA										
Ommastrephidae	94	11	18	1	104	18	51		2	2
Symplectoteuthis spp.	44		24		79		46		2	

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods)

on 58% squid, 28% fish (lanternfishes and bristlemouths), and 12% crustaceans in New Zealand (Imber 1973). The Bonin petrel is unique among *Pterodroma* in its heavy reliance on fish instead of squid.

Gray-backed Tern.—We collected and analyzed 272 regurgitations from gray-backed terns in 1978–80, including each month March–August. Most were collected on Laysan, Lisianski, and Pearl and Hermes Reef, but others were obtained on Nihoa, Necker, and French Frigate Shoals. We collected half of the samples from adult birds and half from dependent young. Samples averaged 4 ml and 8.8 prey items. The sample condition was generally very good, and 96% of the fishes could be identified at least to family.

We found the volume of the prey to be 92% fish, 4% squid, and 3% crustaceans. The diet proved to be complex, consisting of 41 families of fish (the highest for any species in this study), 3 mollusk families, 5 groups of crustaceans, 3 insects, and a coelenterate (Table 28). The highest-ranked prey item was a cowfish, which occurred in two-thirds of the samples and accounted for 42% of the sample volume. The next ranked family was flyingfishes. Most of the 167 specimens we obtained could not be identified further, but 17 were identified as *Cypselurus* spp. Goatfishes ranked third. Dolphin-fishes ranked fourth and consisted of both *Coryphaena hippurus* and *C. equiselis.* Round herrings, crabs, and man-o-war fish (Fig. 11) also ranked high in the diet.

We obtained 1,092 reliable prey lengths. The smallest was a 3-mm sea-strider and the largest a 138-mm blue marlin, with an average of 20 mm. The cowfish had a mean length of 15 mm and ranged as large as 25 mm (Table 29). Except for the crab megalopa and insects, most common prey items had average lengths 15–40 mm, including flyingfishes (*Cypselurus* spp., 38 mm), dolphin-fish (*C. hippurus*, 32 mm), and goatfishes (41 mm).

We collected enough samples to make some geographical and seasonal comparisons, although our analysis suffers from the fact that we could not collect samples during fall. Cowfish ranked first in all areas and seasons except during summer in the Midway Island group. Flyingfishes consistently ranked second or third during the 3 seasons for which we have samples but ranked lowest during spring at Midway. Goatfishes occurred seasonally. Only 1 occured in the 24 samples collected during winter, yet they ranked within the top 3 families during spring and summer in both the Laysan and French Frigate Shoals regions. At Midway, they did not occur in any of 24 samples collected during summer. Dolphin-fishes generally ranked high

Table 26. Prey items identified to lowest taxon in 144 Bonin petrel samples. See Table 3 for method of calculating rank.

Prey	Rank	No of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Blenniidae	26	1	0.7	<0.1
Carangidae	26	1	0.7	<0.1
Congridae	16.5	3	2.1	0.5
Exocoetidae	21	2	1.4	0.1
Gempylidae	14			
Gempylus serpens		4	2.8	0.3
Unidentified gempylid		1	0.7	0.2
Gonostomatidae	10			
Vinciguerria spp.		21	6.3	1.2
V. nimbaria		4	1.4	0.4
Holocentridae	26	1	0.7	<0.1
Monacanthidae	20	2	0.7	0.6
Mullidae	7.5	36	7.6	2.4
Myctophidae	4			
Hygophum sp.		1	0.7	<0.1
Myctophum sp.		1	0.7	<0.1
Unidentified myctophid		76	33.3	14.1
Sternoptychidae	5			
Argyropelecus spp.		2	1.4	0.1
Unidentified sternoptychid		56	24.3	6.6
Synodontidae	13	40	2.1	1.3
Pleuronectoidei (flatfish)	26	1	0.7	<0.1
Unidentified fishes	2	87	47.2	19.9
MOLLUSCA				
Decapoda				
Ommastrephidae	11.5	11	4.0	2.0
Enoploteuthidae	26			
Pterygioteuthis microlampas		1	0.7	<0.1
Histioteuthidae	22	1	0.7	0.4
Unidentified squid	1	113	61.1	18.5
CRUSTACEA				
Mysidacea	15			
Gnathophausia spp.		2	1.4	0.2
Unidentified mysid		1	0.7	0.5
Euphausiacea	26	1	0.7	<0.1
Amphipoda	11.5			
Oxycephalidae		1	0.7	<0.1
Unidentified amphipod		12	6.9	1.1
Isopoda	19			
Anuropus sp.		1	0.7	0.3
Parasitic isopod		2	1.4	<0.1
Copepoda	18			
Calanoid copepod		1	0.7	<0.1
Parasitic copepod		2	1.4	0.1
Unidentified copepod		1	0.7	0.1
Shrimp	9	40	6.3	1.6
Crab	16.5			
Crab megalopa		4	1.4	0.3
Galatheidae		1	0.7	<0.1
Unidentified crustacean	6	27	13.9	2.6
INSECTA				
Gerridae	7.5			
Halobates sericeus		84	16.7	0.5
TUNICATA				
Pyrosomatidae	26	1	0.7	<0.1
UNIDENTIFIED REMAINS	3	69	50.7	23.5

only during spring and summer in the Laysan and Midway Island groups. Round herrings ranked high during summer at Midway. They occurred only in small numbers elsewhere and were found in but 1 of 161 samples collected in the Laysan Island group. Man-o-war fish did not occur during winter, ranked second during summer at Midway, and yet did not occur at Laysan during that season. Crabs occurred in small numbers in most areas and seasons sampled, but ranked highest during spring at Midway. Striped hawkfish, bristlemouths, and flying gurnards ranked high at certain locations during a single season. We conclude that gray-backed terns fed heavily at all times on cow fish. There are no previous studies of the diet of this species, but Munro (1944:61) found it fed on 100-mm squid and Clapp (1976) reported it fed on lizards.

White Tern (Fairy Tern).—We collected 241 samples from white terns, most coming from Midway, Laysan, and French Frigate Shoals, with others collected on Lisianski and Kure Islands. Samples were collected during 1978–80 and represent each month except December. We obtained samples from adults (43%), nestlings (24%), and from dropped items beneath roosts or nests (33%). Sample volumes averaged 3.8 ml and contained a mean of 2.6 prey items. Sample condition was excellent, and 98% of the fishes obtained were identified to family.

By volume, the samples consisted of 88% fish, 12% squid, and 0.4% crustaceans. We identified 33 fish families, 1 squid family, and shrimp (Table 30). Goatfishes ranked highest, followed by flyingfishes. *E. volitans* accounted for two-thirds of those flyingfishes that could be identified to genus, and much of the rest were *Cypselurus* spp. Ommastrephid squids ranked third and consisted of *S. oualaniensis* and *H. pelagicus*. The fourth ranking family was the dolphin-fishes, which was represented by nearly equal numbers of *Coryphaena hippurus* and *C. equiselis*. Other common prey included needlefish, halfbeaks, and silversides.

We obtained 319 length measurements and 142 volume measurements for various

Table 27. Lengths and volumes of some prey items[a] of the Bonin petrel. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Mullidae	9		46		56		51		1	
SQUID										
Ommastrephidae	6		20		72		46		7	
CRUSTACEA										
Anuropus sp.	1	1	54	5	54	5	54	5		
Amphipoda	3		11		40		23		9	
Crab megalopa	3		7		7		7		0	
INSECTA										
Halobates sericeus	18	2	3	0.1	4	0.1	4	<0.1		0

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

prey items. Lengths averaged 46 mm and ranged from a 12-mm snake mackerel to a 200-mm needlefish. Most of the important prey items averaged 30–80 mm, including goatfishes (35 mm), ommastrephid squids (50 mm), and *Cypselurus* spp. (80 mm) (Table 31). We included all samples for this analysis, even some dropped fishes collected under roosting young that may have been too long for them to swallow. However, it seems unlikely that a tern would take a fish that would be too long for adult consumption. Some nestlings were seen perched with a fish tail protruding from the bill, indicating that some long fishes were consumed by the young.

Our sampling was throughout the year only in the Midway Island group and was generally restricted to spring and summer for the Laysan and French Frigate Shoals groups. Our results concerning seasonal and geographical patterns are difficult to interpret because the diet of this species is particularly varied. Flyingfishes were not found in any of 16 samples taken during winter. One flyingfish was found in 17 samples collected during spring at Midway, yet this family ranked second highest at both Laysan and French Frigate Shoals in that season. Flyingfishes were most common during summer, ranking first or second in each of the 3 island groups. Goatfishes ranked first during spring at each island group. During summer they were not present in any of 50 samples taken at Midway, yet they ranked first in the Laysan Island group. The ranking of ommastrephid squids shows no pattern, but they commonly occurred in all island groups and seasons. Dolphin-fishes did not occur anywhere during winter, nor at Midway or French Frigate Shoals during spring. However, this family ranked high during both spring and summer at Laysan. The young of the striped hawkfish ranked high, especially at Midway, during winter and spring but did not occur during summer or fall. Silversides ranked high during summer at Midway, but were never common elsewhere. Lanternfishes only occurred at the Midway Island group, where they ranked first during spring. Anchovies occurred only at Midway during fall, where they ranked first. Snake mackerels, lizardfishes, bristlemouths, halfbeaks, and needlefishes ranked within the top 5 prey during certain seasons at certain island groups. These findings indicate that white terns prey opportunistically on most any species of appropriate size that is available in surface waters, especially those between 30–80 mm.

The white tern has a diversified diet wherever it has been studied. It fed on at least 16 fishes at Ascension Island, principally cutlass fishes, blennies, and flyingfishes (Stonehouse 1962, Dorward 1963*b*).

Table 28. Prey items identified to lowest taxon in 272 gray-backed tern samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Ammodytidae	52.5			
Bleekeria gillii		1	0.4	<0.1
Atherinidae	52.5			
Pranesus insularum		1	0.4	<0.1
Balistidae	13			
Xanthichthys mento		11	2.6	1.4
Unidentified balistid		15	2.6	0.3
Belonidae	42.5			
Ablennes hians		1	0.4	<0.1
Unidentified belonid		1	0.4	<0.1
Blenniidae	34	3	1.1	0.2
Bramidae	42.5			
Brama orcini		1	0.4	<0.1
Pteraclis velifer		1	0.4	0.1
Carangidae	9			
Decapterus spp.		19	2.6	0.3
D. macrosoma		1	0.4	0.1
Naucrates ductor		10	3.3	0.3
Seriola spp.		10	1.5	0.3
Carangoides ferdau		1	0.4	0.1
Unidentified carangid		9	2.9	0.8
Chaunacidae	16	75	3.3	1.0
Cheilodactylidae	14.5			
Cheilodactylus vittatus		22	4.8	1.4
Clupeidae	5			
Spratelloides delicatulus		182	6.6	5.4
Congridae	48	1	0.4	0.1
Coryphaenidae	4			
Coryphaena spp.		19	5.1	0.7
C. hippurus		76	11.4	2.3
C. equiselis		57	4.0	0.8
Dactylopteridae	28			
Dactyloptena orientalis		7	1.1	0.4
Diodontidae	18.5			
Diodon spp.		5	1.8	0.3
Unidentified diodontid		9	2.6	0.4
Echeneidae	46.5			
Rhombochirus osteochir		2	0.7	<0.1
Exocoetidae	2			
Parexocoetus brachypterus		1	0.4	0.3
Exocoetus monocirrhus		1	0.4	0.2
Prognichthys gilberti		4	1.5	0.4
Cypselurus spp.		17	4.8	1.4
Unidentified exocoetid		143	26.8	7.1
Gempylidae	22			
Gempylus serpens		9	2.6	0.8
Gonorhynchidae	52.5			
Gonorhynchus gonorhynchus		1	0.4	<0.1
Gonostomatidae	21			
Vinciguerria nimbaria		20	1.5	1.1
Hemiramphidae	53			
Oxyporhamphus micropterus		1	0.4	<0.1
Holocentridae	30	8	1.1	0.2
Istiophoridae	17			
Istiophorus platypterus		3	0.7	0.2
Tetrapterus angustirostris		1	0.4	0.1
Makaira nigricans		3	1.1	0.4
Unidentified istiophorid		6	2.2	0.3
Kyphosidae	29			
Kyphosus bigibbus		5	1.5	0.4
Macrorhamphosidae	18.5			
Macrorhamphosus gracilis		17	4.0	0.7
Macrouridae	52.5	1	0.4	<0.1
Monacanthidae	23			
Pervagor spilosoma		3	0.7	0.4
Alutera scripta		5	0.7	0.2
Unidentified monacanthid		2	0.7	0.1
Mugilidae	27	7	1.5	0.3
Mullidae	3	173	16.9	7.4
Myctophidae	20	11	2.9	0.9
Nomeidae	8			
Nomeus gronovii		48	6.3	2.3
Psenes cyanophrys		2	0.7	0.1
Unidentified nomeid		65	4.0	1.0
Ostraciontidae	1			
Lactoria fornasini		708	66.5	41.8
Pegasidae	10			
Pegasus papilio		48	8.8	2.3
Pomacentridae	31	7	1.5	0.1
Priacanthidae	39	2	0.7	0.4
Scombridae	45			
Katsuwonus pelamis		2	0.4	<0.1
Unidentified tuna		1	0.4	<0.1
Serranidae	49			
Odontanthias elizabethae		2	0.4	<0.1
Soleidae	42.5			
Aseraggodes kobensis		1	0.4	<0.1
Unidentified soleid		1	0.4	0.1
Sphyraenidae	46.5	2	0.7	<0.1
Sternoptychidae	26			
Sternoptyx diaphana		1	0.4	0.4
Unidentified sternoptychid		4	1.5	0.3
Synodontidae	32	5	1.8	0.1
Tetraodontidae	36.5			
Lagocephalus lagocephalus		1	0.4	0.1
Unidentified tetraodontid		3	0.7	<0.1
Xiphiidae	24			
Xiphias gladius		7	2.6	0.5
Unidentified fishes	6.5	83	19.1	2.5
MOLLUSCA				
Decapoda				
Ommastrephidae	14.5			
Symplectoteuthis spp.		2	0.7	0.1
Unidentified ommastrephid		15	4.4	2.0
Unidentified squids	11	29	7.0	1.7
Janthinidae	40			
Janthina spp.		2	0.4	0.1

Table 28. Continued.

Table 28. Continued.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
J. pallida		2	0.4	<0.1
J. prolongata		1	0.4	<0.1
Cavolinidae	53			
Cavolinia tridentata		1	0.4	<0.1
CRUSTACEA				
Euphausiacea	36.5	14	0.4	0.1
Isopoda	35			
Parasitic isopod		3	1.1	<0.1
Unidentified isopod		3	0.7	<0.1
Copepoda	53			
Pontellidae				
Pontella atlantica		1	0.4	<0.1
Shrimp	33	5	1.5	0.1
Crab	6.5			
Brachyura		6	2.2	0.4
Unidentified megalopa		167	6.3	2.2
Portunidae				
Planes cyaneus		6	1.1	0.4
Portunid megalopa		1	0.4	<0.1
INSECTA				
Gerridae	12			
Halobates sericeus		135	9.9	0.6
Lepidoptera (moth)		2	0.7	<0.1
Orthoptera (grasshopper)				
Euconocephalus nasutus		1	0.4	0.1
COELENTERATA				
Velellidae	25			
Velella velella		11	1.8	0.2
UNIDENTIFIED REMAINS	42.5	2	0.7	0.1

Dorward also found that it ate hatchetfishes and lanternfishes. On Christmas Island (Pacific), white terns fed about half on ommastrephid squids and half on fishes by volume (Ashmole and Ashmole 1967*b*). A wide variety of fishes was consumed there, among which the most important were blennies, flyingfishes, halfbeaks, lanternfishes, and bristlemouths. In Hawaii, white terns have been reported to feed on halfbeaks (Fisher 1903:785), anchovies, and silversides (Anderson 1954). All workers have found the condition of prey taken from this species to be excellent due to its habit of bringing fishes to young crosswise in the bill, and such specimens have been used to identify new fish species (Tyler and Paxton 1979).

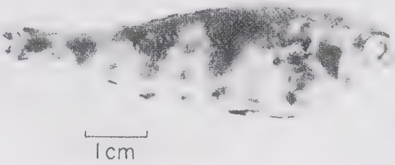

Fig. 11. Man-o-war fish, a prey item.

Black Noddy.—During 1978–80 we collected 494 samples (the largest sample size in this study) from black noddies, most coming from Laysan, Lisianski, and French Frigate Shoals. Other samples were collected on Kure, Midway, and Pearl and Hermes Reef. Collections included samples from all 12 months. We collected samples from both adults (79%) and dependent young (21%). The samples averaged 5 ml and 12.6 prey items. We identified 94% of the fishes to family or better.

By volume, the prey was 92% fish, 7% squid, and 1% crustaceans. We were able to identify 36 fish families, 2 squid families, 3 groups of crustaceans, and an insect (Table 32). The highest ranked prey family was goatfishes, followed by lizardfishes. Round herrings (Fig. 12) ranked third. Next were flyingfishes, of which the most common of the 5 species identified was *E. volitans* (Table 32). Other common prey items included gobies, ommastrephid squids, and snake mackerels.

We had 1,038 prey items for which we could make reliable length measurements. These items averaged 34 mm and ranged from a 5-mm crab megalopa to a 167-mm leptocephalus larvae. The highest ranked taxa had mean lengths in the 20–50 mm range and included ommastrephid squids (32 mm), lizardfishes (38 mm), and goatfishes (45 mm) (Table 33). We made 142 reliable volumetric measurements.

Although sampling was inadequate for some areas and seasons, several generalizations can be made regarding geographical and seasonal changes in diet. Goatfishes ranked first or second in each season in the Laysan Island group. At French

Table 29. Lengths and volumes of some prey items[a] of the gray-backed tern. Length and volume values are not necessarly for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Seriola spp.	10	3	18	0.3	32	0.7	23	0.5	1	<0.5
Mullidae	14	3	28	0.7	65	2.1	41	1.3	3	<0.5
Balistidae	10	3	6	0.2	23	0.5	16	0.4	2	<0.5
Xanthichthys mento	11	8	15	0.4	34	2.3	24	1 1	2	<0.5
Chaunacidae	34		6		13		9		<0.5	
Coryphaena hippurus	35	5	14	0.3	57	1.5	32	0.7	2	<0.5
C. equiselis	43	33	15	0.1	48	1	24	0.2	1	0
Spratelloides delicatulus	67	70	18	0.1	51	1.7	38	0.7	1	0
Exocoetidae	28	14	13	0.1	42	0.9	26	0.4	2	0
Cypselurus spp.	11	5	29	0.4	63	0.7	38	0.6	3	0
Nomeidae	23	3	10	0.1	42	0.3	22	0.2	2	0
Nomeus gronovii	21	19	18	0.1	48	1.5	29	0.4	2	<0.5
Lactoria fornasini	535	123	7	0.1	25	1.5	15	0.5	<0.5	0
Pegasus papilio	44	2	8	0.1	24	0.1	16	0.1	<0.5	0
CRUSTACEA										
Crab megalopa	14	7	5	0.1	15	0.2	9	0.1	1	0
INSECTA										
Halobates sericeus	34	22	3	0.1	4	0.1	4	0.1	<0.5	0

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

Frigate Shoals, they ranked third in all seasons except spring, when they ranked first. In the Midway Island group, goatfishes occurred only during spring and were absent from all 28 samples taken in the remainder of the year. Lizardfishes ranked high during each season in the Laysan and French Frigate Shoals regions, either first or second. They also ranked second during fall and winter in the Midway Island group, and their apparent absence during spring and summer there may be an artifact of inadequate sampling. Round herrings were not found in any of the 76 samples collected during winter, yet ranked third and fourth during spring and summer at Laysan and French Frigate Shoals. Flyingfishes were very common during summer, ranking first at French Frigate Shoals. Bristlemouths were commonly eaten during winter at Midway and Laysan while during the same season at French Frigate Shoals gobies ranked very high. Ommastrephid squids ranked third or fourth at several locations during fall, winter, and spring. Our data indicate that black noddies fed most heavily on goatfishes and lizardfishes throughout the Hawaiian Archipelago throughout the year. Other prey in the 20–50 mm size range were also taken.

The diet of black noddies in Hawaii is unique because of the common occurrence of goatfishes, lizardfishes, and round herrings. At Ascension (Stonehouse 1962) and Christmas Island (Ashmole and Ashmole 1967*b*), black noddies fed on flyingfishes, halfbeaks, blennies, and an anchovy (*Engraulis* sp). This bird has been reported feeding on *Stolephorus delicatulus* (we believe this could be *Stolephorus buccaneeri* or *Spratellodes delicatulus*) in the Marshall Islands (Marshall 1951).

Bulwer's Petrel.—During 1978–80 we could collect only 100 samples from Bulwer's petrels. Samples were taken during the breeding season, May–September, because this species rarely comes to land in other months. Most samples were collected on Laysan, but 2 were obtained on Nihoa. Sample condition was generally poor,

Table 30. Prey items identified to lowest taxon in 241 white tern samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Atherinidae	7.5			
Pranesus insularum		16	3.3	3.2
Belonidae	6			
Ablennes hians		17	5.4	3.9
Unidentified belonid		1	0.4	<0.1
Blenniidae	15			
Plagiotremus goslinei		3	0.8	0.5
Unidentified blenniid		9	1.7	1.1
Bramidae	30.5			
Pteraclis velifer		1	0.4	0.4
Canthigasteridae	33.5			
Canthigaster sp.		1	0.4	0.2
Carangidae	7.5			
Decapterus sp.		1	0.4	0.4
D. macrosoma		3	0.4	0.1
Naucrates ductor		6	1.7	0.7
Seriola sp.		1	0.4	0.4
Caranx spp.		2	0.8	0.8
Unidentified carangid		1	0.4	0.4
Chaetodontidae	35			
Chaetodon sp.		1	0.4	0.1
Cheilodactylidae	11.5			
Cheilodactylus vittatus		8	3.3	2.9
Clupeidae	15			
Spratelloides delicatulus		13	2.1	1.6
Coryphaenidae	5			
Coryphaena spp.		3	0.8	0.4
C. hippurus		8	2.1	1.7
C. equiselis		9	3.7	2.2
Diodontidae	25.5			
Diodon sp.		1	0.4	0.4
Unidentified diodontid		1	0.4	0.1
Echeneidae	19			
Rhombochirus osteochir		6	2.1	0.7
Remora sp.		1	0.4	<0.1
Unidentified echeneid		2	0.8	<0.1
Engraulidae	21			
Stolephorus buccaneeri		13	0.8	0.8
Exocoetidae	2			
Parexocoetus brachypterus		2	0.8	0.2
Exocoetus volitans		66	8.7	6.8
E. monocirrhus		2	0.8	0.8
Prognichthys gilberti		2	0.8	0.7
Cypselurus spp.		17	7.1	6.0
C. speculiger		2	0.8	0.8
C. atrisignis		1	0.4	0.4
Unidentified exocoetid		44	12.9	6.6
Gempylidae	13			
Gempylus serpens		11	2.9	1.3
Unidentified gempylid		3	0.4	0.1
Gonorhynchidae	25.5			
Gonorhynchus gonorhynchus		2	0.8	0.5
Hemiramphidae	6			
Euleptorhamphus viridis		4	1.2	1.2
Hyporhamphus acutus pacificus		9	2.5	1.6
Oxyporhamphus micropterus		7	2.5	1.5
Unidentified hemiramphid		3	0.8	0.2
Holocentridae	17			
Myripristis chryseres		1	0.4	0.4
Unidentified holocentrid		11	1.7	1.4
Hoplichthyidae	30.5			
Hoplichthys sp.		1	0.4	0.4
Istiophoridae	11.5			
Istiophorus platypterus		8	2.9	2.8
Makaira nigricans		1	0.4	<0.1
Macrorhamphosidae	24			
Macrorhamphosus gracilis		3	1.2	0.9
Monacanthidae	30.5			
Cantherhines sp.		1	0.4	0.4
Mugilidae	20	5	1.7	1.3
Mullidae	1	185	29.5	19.5
Myctophidae	15			
Benthosema fibulatum		1	0.4	0.4
Unidentified myctophid		6	2.5	2.5
Nomeidae	23			
Nomeus gronovii		3	1.2	0.9
Unidentified nomeid		1	0.4	0.2
Pomacentridae	22			
Chromis vanderbilti		1	0.4	0.1
C. struhsakeri		1	0.4	0.4
Unidentified pomacentrid		3	1.2	0.5
Scombridae	27			
Katsuwonus pelamis		1	0.4	0.2
Unidentified tuna		1	0.4	0.1
Serranidae	33.5			
Grammatonotus laysanus		1	0.4	0.2
Soleidae	36.5	1	0.4	0.1
Synodontidae	9			
Synodus sp.		1	0.4	0.4
Unidentified synodontid		21	3.7	1.0
Tetraodontidae	30.5	1	0.4	0.4
Xiphiidae	36.5			
Xiphias gladius		1	0.4	0.1
Unidentified fishes	10	13	5.0	1.5
MOLLUSCA				
Decapoda				
Ommastrephidae	3			
Symplectoteuthis spp.		5	1.7	1.7
S. oualaniensis		1	0.4	0.4
Hyaloteuthis pelagicus		2	0.4	0.4
Unidentified ommastrephid		32	9.5	7.9
Unidentified squids	18	8	3.3	1.2
CRUSTACEA				
Shrimp	28			
Penaeidae				
Gennadus sp.		1	0.4	0.1
Unidentified penaeid		1	0.4	0.1

Table 31. Lengths and volumes of some prey items[a] of the white tern. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Mullidae	89	38	15	0.1	65	4	35	1.2	1	<0.5
Pranesus insularum	9	7	22	0.1	63	3	45	1.1	5	<0.5
Ablennes hians	4	6	98	0.8	200	11	141	5.3	21	2
Spratelloides delicatulus	9	2	18	0.1	51	1	29	0.8	4	1
Exocoetidae	11		17		104		38		8	
Exocoetus volitans	39	19	15	0.1	107	9	42	0.8	5	1
Cypselurus spp.	13	2	22	0.2	114	0.8	80	0.5	9	<0.5
MOLLUSCA										
Ommastrephidae	24	10	14	0.2	99	16	50	7.5	6	2

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

with many regurgitations being rejected in the field because they were only oil or because the prey items were digested beyond recognition. We also experienced difficulty in getting this species to regurgitate. Most samples (78%) were taken from adult birds, but 22% came from nestlings. The relatively poor condition is reflected in the fact that by volume 5% of the samples were unidentified remains, 20% were unidentified squids, and 30% were unidentified fishes. However, 67% of the individual fishes collected were identified to family or better. It is likely that some of the unidentified fishes were midwater species for which we lacked a reference collection of skeletal material. Food samples from this bird yielded an average volume of 3 ml and contained an average of 3.9 prey items.

We found 7 fish families, 1 squid family, a gastropod, an annelid, 4 groups of crustaceans, and an insect (Table 34). By volume, ignoring stomach oil and unidentified remains, the prey was 71% fish, 22% squid, 4% crustaceans, and 3% sea-striders. The 2 highest ranked categories were unidentified fishes and squids. These categories are artificially high because they pool unidentified material from numerous families and species. The highest ranked family was lanternfishes, and 5 genera were identified (Table 34). The next highest item was the hatchetfishes, where *Argyropelecus* spp. was common. Other common prey included sea-striders and flyingfish ova. We found small plastic particles in some of the samples which, as in the albatrosses, could have been ingested while feeding on fish eggs that were attached to these floating particles.

We had measurements of only 30 prey lengths. These averaged 23 mm and ranged from a 3-mm sea-strider to a 130-mm flyingfish. Five ommastrephid squids had a mean length of 57 mm (range 38–68 mm).

The distribution of sampling made it impossible to draw conclusions for any area except Laysan Island. There, 16 samples were collected during spring and 82 during summer. Bulwer's petrels fed more on squids during spring (61% by volume) than summer (13%). During summer, lanternfishes (20%) and hatchetfishes (19%) were common prey. The samples contained no midwater fishes during spring. Sea-striders ranked high during both seasons. Bulwer's petrels fed primarily on squids and mesopelagic fishes, most of which were <100 mm in length. There are no previous published accounts of the diet of this species, but *B. fallax* eats 20-mm squid (Bailey and Bourne 1963).

Sooty Storm-petrel.—During 1979–81, 8 samples from sooty storm-petrels were collected January–May at Laysan, and 2 were collected during February 1981 at

Table 32. Prey items identified to lowest taxon in 494 black noddy samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Ammodytidae	29			
Bleekeria gillii		5	0.4	0.2
Atherinidae	14.5			
Pranesus insularum		27	2.0	1.8
Balistidae	45.5	1	0.2	<0.1
Belonidae	28			
Platybelone argalus platyura		2	0.4	0.2
Ablennes hians		2	0.4	<0.1
Blenniidae	25	11	1.0	0.2
Bothidae	38	3	0.4	<0.1
Carangidae	12			
Decapterus spp.		22	1.4	0.3
D. macrosoma		7	0.8	0.4
D. tabl		2	0.4	0.1
Naucrates ductor		8	1.2	0.3
Unidentified carangid		12	1.4	0.3
Cheilodactylidae	16			
Cheilodactylus vittatus		23	3.0	0.8
Cirrhitidae	34	4	0.6	<0.1
Clupeidae	3			
Spratelloides delicatulus		560	11.9	10.2
Coryphaenidae	19			
Coryphaena spp.		6	1.2	0.4
C. hippurus		2	0.4	0.1
C. equiselis		11	1.8	0.3
Dactylopteridae	41			
Dactyloptena orientalis		1	0.2	0.1
Echeneidae	39.5			
Remora remora		1	0.2	<0.1
Rhombochirus osteochir		1	0.2	<0.1
Engraulidae	26			
Stolephorus buccaneeri		25	1.0	0.1
Exocoetidae	4.5			
Parexocoetus brachypterus		4	0.2	0.1
Exocoetus volitans		31	2.2	1.2
Prognichthys gilberti		1	0.2	0.1
Cypselurus spp.		7	1.4	0.5
C. atrisignis		1	0.2	<0.1
Unidentified exocoetid		286	18.2	6.3
Gempylidae	8			
Gempylus serpens		104	13.4	2.1
Unidentified gempylid		2	0.4	0.1
Gobiidae	6			
Ptereleotris heteropterus		435	11.7	2.8
Gonorhynchidae	10			
Gonorhynchus gonorhynchus		85	6.5	1.8
Hemiramphidae	23			
Euleptorhamphus viridis		2	0.4	<0.1
Oxyporhamphus micropterus		4	0.4	0.2
Unidentified hemiramphid		4	0.6	<0.1
Holocentridae	9			
Sargocentron sp.		1	0.2	<0.1
Unidentified holocentrid		112	9.1	1.4
Istiophoridae	30			
Makaira nigricans		3	0.4	<0.1
Unidentified istiophorid		2	0.4	0.1
Kyphosidae	32			
Kyphosus bigibbus		4	0.2	0.2
Macrorhamphosidae	20			
Macrorhamphosus gracilis		13	2.6	0.6
Molidae	24			
Ranzania laevis		9	1.2	0.4
Monacanthidae	37			
Pervagor spilosoma		2	0.2	0.2
Mugilidae	45.5	1	0.2	<0.1
Mullidae	1	1,204	49.8	31.2
Myctophidae	33	6	0.2	0.1
Nomeidae	17.5			
Nomeus gronovii		9	1.6	0.5
Psenes cyanophrys		4	0.4	0.1
Unidentified nomeid		7	0.8	0.2
Pomacentridae	31			
Chromis sp.		1	0.2	<0.1
Unidentified pomacentrid		5	1.0	<0.1
Scomberesocidae	39.5			
Cololabis saira		2	0.4	<0.1
Scombridae	13			
Katsuwonus pelamis		9	1.0	0.1
Thunnus alalunga		5	0.4	0.1
Unidentified tuna		20	2.4	<0.1
Unidentified scombrid		15	1.8	0.1
Scombrid larvae		6	0.4	<0.1
Tuna larvae		18	0.8	0.1
Sphyraenidae	35.5	2	0.4	0.1
Sternoptychidae	42	2	0.2	<0.1
Synodontidae	2	2,365	45.3	20.7
Tetraodontidae	45.5			
Lagocephalus lagocephalus		1	0.2	<0.1
Unidentified fishes	4.5	340	22.3	4.3
Leptocephalus larvae	14.5	36	4.3	0.4
Anguilliformes	45.5	1	0.2	<0.1
Pleuronectoidei (flatfish)	45.5	1	0.2	<0.1
MOLLUSCA				
Decapoda				
Ommastrephidae	7			
Symplectoteuthis spp.		10	1.8	0.8
S. oualaniensis		1	0.2	0.2
Unidentified ommastrephid		93	11.1	3.9
Onychoteuthidae	35.5			
Onykia spp.		2	0.4	0.1
Unidentified squids	11	69	10.3	1.8
CRUSTACEA				
Stomatopoda	22			
Pseudosquilla sp.		1	0.2	<0.1
Squilla spp.		12	1.8	0.1
Lysiosquilla spp.		2	0.2	0.1
Coronida sp.		1	0.2	<0.1
Unidentified stomatopod		3	0.6	<0.1
Shrimp	17.5			

Table 32. Continued.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
Penaeidae				
Penaeus marginatus		15	0.6	<0.1
Unidentified penaeid		4	0.4	<0.1
Aristaeidae		1	0.2	<0.1
Caridea		31	0.2	0.1
Unidentified shrimps		20	2.8	0.1
Crab megalopa	21	34	1.4	0.2
INSECTA				
Caterpillar	45.5	1	0.2	<0.1
UNIDENTIFIED REMAINS	27	4	0.8	0.2

Nihoa. This species breeds only in inaccessible islands during winter and spring, making sampling difficult. We also had difficulties inducing birds to regurgitate, and many of the samples that we did collect were entirely stomach oil. All samples came from adults. The advanced state of digestion of the samples made identification difficult, but aside from unidentified remains and stomach oil, we found 23% fish, 29% squid, 12% coelenterates, and 5% crustaceans by volume (Table 35). We could not identify any squid family and identified only 1 fish family, the hatchetfishes. Wind-sailers and sea-striders ranked high among prey items. These data give an indication of the types of prey eaten by this species, but the unlikely result that the common seabird tick accounted for 10% of the volume emphasizes the fact that conclusions must be limited. Small plastic particles occurred in samples from this species.

The length measurements of only 7 prey items were taken that averaged 11 mm and ranged from a 2-mm tick to a 27-mm wind-sailer. We do not have enough information to draw any conclusions concerning geographical or seasonal changes in the diet of sooty storm-petrels.

Blue-gray Noddy.—We collected 111 samples from blue-gray noddies from 1978–81. Because of the limited distribution of this species, all samples were collected on Nihoa (46%) and Necker (54%). We could obtain samples only during February, May, June, and August. Except for 4 samples, all were taken from adult birds (96%). The samples had a mean volume of 1.8 ml and averaged 55 prey items. Even eliminating the large numbers of sea-striders, the blue-gray noddy had an average of 31 prey items/sample, by far the largest number for any of the 18 seabirds in this study. The condition of the samples was relatively good, yet only 46% of the fishes could be identified to family because of their extremely small size.

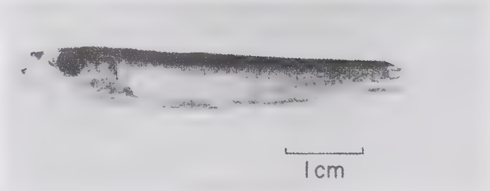

Fig. 12. Round herring, a prey item.

By volume, our samples were 61% fish, 1.5% squid, 18% crustacean, and 19% insect. We could identify 28 fish families, 1 squid family, 8 groups of crustaceans, 2 coelenterates, and a marine insect (Table 36). The highest ranking prey item was sea-striders, which occurred in 81% of the stomachs sampled and accounted for 19% of the prey volume. Unidentified fishes ranked second. These accounted for 16% of the prey volume and were therefore a substantial component of the diet, but probably included many families and species. Lizardfishes ranked third. Flyingfishes and goatfishes also were common. Copepods, almost exclusively *Pontella atlantica*, ranked seventh. This species was reported by Wilson (1950) in the Hawaiian Archipelago and is associated with surface waters around islands. Stomatopods also were common and included 5 genera, especially *Pseudosquilla* and *Coronida*.

Blue-gray noddies ate the smallest fishes and invertebrates of all seabirds in this study. We measured 635 prey items. They averaged 10 mm, ranging from a 2-mm sea-strider to a 50-mm halfbeak. The most

Table 33. Lengths and volumes of some prey items[a] of the black noddy. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Holocentridae	44		9		56		19		2	
Mullidae	95	7	20	0.3	61	3	45	1.5	1	<0.5
Pranesus insularum	11		32		86		64		4	
Spratelloides delicatulus	130	20	29	0.2	61	3	45	1.5	1	<0.5
Exocoetidae	32		18		52		33		2	
Exocoetus volitans	23		32		67		48		2	
Ptereleotris heteropterus	161	54	13	0.1	35	0.3	27	0.2	<0.5	0
Synodontidae	266	21	25	0.1	65	1	38	0.4	<0.5	0
MOLLUSCA										
Ommastrephidae	48		11		67		32		1	
CRUSTACEA										
Stomatopod larvae	9		11		40		23		4	
Caridean shrimp	22		9		9		9		0	
Squilla spp.	10	4	12	0.1	41	0.2	35	0.1	3	0

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods)

common fishes had average lengths 10–30 mm, including flyingfishes (16 mm), goatfishes (18 mm), and lizardfishes (32 mm). The crustaceans and insects were smaller: *Pseudosquilla* spp. (9 mm), *Pontella atlantica* (5 mm), and sea-striders (3 mm). These lengths and displacement volume data, where many common prey items had mean volumes <0.1 ml, give a good indication of the minute prey on which blue-gray noddies fed (Table 37).

We cannot make any geographical comparisons, but we can draw some tentative conclusions concerning seasonality in the diet of the blue-gray noddy. Comparing winter with spring, the only similarities are the high rankings of unidentified fishes and lizardfishes. During winter, blue-gray noddies fed on shrimp, flounder larvae, and squids. During spring sea-striders, flyingfishes, and goatfishes ranked high. Few samples were collected during winter, but it is probable that this species fed most heavily on lizardfishes, supplementing this with various other items. The small prey size and reliance on crustaceans and insects is consistent with the findings of Ashmole and Ashmole (1967*b*). At Christmas Island, they fed on fish (75%), squid (10%), and other invertebrates (16%) (Ashmole and Ashmole 1967*b*). Snake mackerels ranked highest among the fishes, followed by flyingfishes, tunas, and blennies. Sea-striders (*H. micans*) and copepods (*Pontella* sp.) also were common. These findings are similar to ours, but Hawaiian birds also fed on lizardfishes and goatfishes.

Prey Length Comparisons

Prey length comparisons, using all prey from all taxa of grades 1 and 2, indicate that larger predators take larger prey (Fig. 13). It is useful to compare the same prey taken by seabirds with similar diets during the spring–summer chick feeding period (Fig. 6). Masked boobies took larger flyingfishes than the other 4 pelecaniforms (ANOVA, $P < 0.001$), which had no statistical differences among them. Pooling all *Decapterus* spp., the smallest 4 species again had no differences among them, but the masked booby fed on larger fishes (ANOVA, $P < 0.01$). Masked and brown boobies had no significant difference between them for ommastrephid squids, nor were there differences among

Table 34. Prey items identified to lowest taxon in 100 Bulwer's petrel samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Carangidae	13			
Decapterus macrosoma		1	1.0	0.4
Exocoetidae	7			
Exocoetus volitans		1	1.0	0.6
Exocoetidae (ova)		6	6.0	3.2
Unidentified exocoetid		2	1.0	0.2
Gonostomatidae	11			
Vinciguerria sp.		1	1.0	0.1
V. nimbaria		2	1.0	<0.1
Diplophos sp.		1	1.0	0.4
Myctophidae	3			
Hygophum spp.		2	2.0	0.4
Myctophum sp.		1	1.0	0.6
Lampanyctus spp.		2	2.0	1.2
Diaphus spp.		3	1.0	0.4
Symbolophorus sp.		1	1.0	0.3
Unidentified myctophid		49	36.0	13.4
Nomeidae	19.5	1	1.0	<0.1
Opisthoproctidae	19.5			
Opisthoproctus sp.		1	1.0	<0.1
Sternoptychidae	4			
Argyropelecus spp.		24	17.0	5.2
Unidentified sternoptychid		41	25.0	10.5
Pleuronectoidei (flatfish)	16.5	1	1.0	0.1
Unidentified fishes	1	67	48.0	29.5
MOLLUSCA				
Decapoda				
Ommastrephidae	10	6	3.0	0.9
Unidentified squids	2	90	46.0	19.8
Gastropoda	16.5	1	1.0	0.1
ANNELLIDA				
Polychaeta	16.5	1	1.0	0.1
CRUSTACEA				
Amphipoda	8	16	5.0	1.5
Copepoda	12	7	1.0	0.1
Shrimp	16.5	1	1.0	0.1
Crab megalopa	14	1	1.0	0.3
Unidentified crustacean	9	8	5.0	1.9
INSECTA				
Gerridae	6			
Halobates sericeus		55	12.0	2.6
UNIDENTIFIED REMAINS	5	13	13.0	5.2

Table 35. Prey items identified to lowest taxon in 10 sooty storm-petrel samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Sternoptychidae	8	1	10.0	10.0
Unidentified fishes	3	5	40.0	13.0
MOLLUSCA				
Unidentified squids	1	7	60.0	28.8
CRUSTACEA				
Euphausiacea	13	1	10.0	0.1
Amphipoda	10	1	10.0	1.3
Isopoda	9	1	10.0	1.7
Shrimp	6	4	20.0	1.5
Unidentified crustacean	11	1	10.0	0.4
INSECTA				
Gerridae	5			
Halobates sericeus		8	30.0	1.1
Caterpillar	12	1	10.0	0.3
TICKS				
Argasidae	7			
Ornithodorus capensis		2	10.0	10.0
COELENTERATA				
Velellidae	2			
Velella velella		9	40.0	11.9
UNIDENTIFIED REMAINS	4	3	30.0	10.1

red-tailed tropicbirds, red-footed boobies, or great frigatebirds. The former 2 species took larger squids than the latter 3 (ANOVA, $P < 0.05$).

There were no significant differences among goatfishes eaten by wedge-tailed shearwaters, Christmas shearwaters, sooty terns, or brown noddies. Black noddies took smaller goatfishes than these 4 species, and white terns ate smaller ones than black noddies (ANOVA, $P < 0.001$). Both shearwaters took larger squids than brown noddies, sooty terns, or white terns, all of which took larger squids than black noddies (ANOVA, $P < 0.001$). Lizardfishes eaten by brown noddies were larger than those taken by black noddies (ANOVA, $P < 0.05$). Flyingfish were taken in successively decreasing lengths by Christmas shearwaters, sooty terns and brown noddies, white terns, and black noddies (ANOVA, $P < 0.05$). Gray-backed terns ate larger prey than blue-gray noddies, including goatfishes (ANOVA, $P < 0.01$), flyingfishes ($P < 0.001$), and crab megalopae ($P < 0.001$).

DISCUSSION

It is evident from the preceding species accounts that the diets of seabirds in the

Table 36. Prey items identified to lowest taxon in 111 blue-gray noddy samples. See Table 3 for method of calculating rank.

Prey	Rank	No. of organisms	Percent of samples in which occurred	Avg % vol
FISHES				
Balistidae	40	2	0.9	<0.1
Belonidae	35			
Ablennes hians		2	0.9	0.1
Blenniidae	18	11	7.2	0.4
Bothidae	13			
Bothidae larvae		6	0.9	0.4
Unidentified bothid		13	5.4	0.9
Carangidae	28			
Naucrates ductor		1	0.9	<0.1
Seriola spp.		3	1.8	0.1
Coryphaenidae	33			
Coryphaena sp.		1	0.9	<0.1
C. hippurus		1	0.9	0.1
Dactylopteridae	21.5			
Dactyloptena orientalis		11	5.4	0.3
Diodontidae	27			
Diodon spp.		6	1.8	0.2
Unidentified diodontid		4	0.9	<0.1
Echeneidae	33			
Rhombochirus osteochir		1	0.9	0.1
Remora sp.		1	0.9	<0.1
Eleotridae	42.5			
Asterropteryx sp.		1	0.9	<0.1
Exocoetidae	4			
Cypselurus sp.		1	0.9	0.2
Unidentified exocoetid		314	45.0	10.7
Gempylidae	11			
Gempylus serpens		13	8.1	1.5
Unidentified gempylid		2	0.9	<0.1
Gobiidae	21.5			
Ptereleotris heteropterus		3	2.7	0.2
Unidentified gobiid		4	2.7	0.2
Gonorhynchidae	33			
Gonorhynchus gonorhynchus		2	1.8	0.1
Hemiramphidae	25			
Euleptorhamphus viridis		2	1.8	0.2
Hyporhamphus acutus pacificus		1	0.9	0.1
Unidentified hemiramphid		4	1.8	0.1
Holocentridae	24	5	4.5	0.5
Istiophoridae	20			
Makaira nigricans		3	2.7	0.4
Istiophorus spp.		2	0.9	0.1
Unidentified istiophorid		1	0.9	0.3
Macrorhamphosidae	37.5			
Macrorhamphosus gracilis		1	0.9	0.1
Mullidae	5	288	42.3	10.4
Nomeidae	29.5			
Nomeus gronovii		2	1.8	0.1
Unidentified nomeid		1	0.9	<0.1
Ostraciontidae	26			
Lactoria fornasini		7	2.7	0.3
Unidentified ostraciontid		1	0.9	<0.1
Pomacentridae	31	2	1.8	0.3
Scomberesocidae	42.5	1	0.9	<0.1
Scombridae	15	11	7.2	0.6
Soleidae	42.5	1	0.9	<0.1
Sphyraenidae	37.5	1	0.9	0.1
Synodontidae	3			
Trachinocephalus myops		1	0.9	<0.1
Unidentified synodontid		319	58.6	14.6
Xiphiidae	14			
Xiphias gladius		11	8.1	0.6
Leptocephalus larvae	29.5	3	2.7	0.1
Unidentified fishes	2	1,259	78.4	16.1
MOLLUSCA				
Decapoda				
Ommastrephidae	37.5	1	0.9	0.1
Unidentified squids	10	34	16.2	1.4
CRUSTACEA				
Crustacean larvae	37.5	1	0.9	0.1
Mysidacea	12			
Siriella spp.		14	3.6	0.2
Unidentified mysid		16	7.2	0.3
Euphausiacea	17	23	7.2	0.3
Stomatopoda	7			
Pseudosquilla spp.		105	12.6	1.6
Squilla spp.		4	3.6	0.3
Lysiosquilla spp.		15	6.3	0.6
Coronida spp.		75	15.3	2.0
Odontodactylus spp.		20	8.1	0.6
Unidentified stomatopod		9	4.5	0.4
Amphipoda	19	25	3.6	0.4
Isopoda	23			
Parasitic isopod		4	3.6	0.2
Unidentified isopod		2	1.8	0.2
Copepoda	6			
Pontellidae		1	0.9	0.1
Pontella spp.		4	2.7	0.3
P. atlantica		319	20.7	2.4
Calanoid copepod		14	2.7	0.3
Unidentified copepod		11	2.7	0.3
Shrimp	8			
Sergestidae		22	0.9	0.2
Lucifer spp.		13	4.5	0.2
Unidentified shrimps		88	42.3	3.2
Crab megalopa	9	247	28.8	3.7
INSECTA				
Gerridae	1			
Halobates sericeus[a]		2,652	81.1	18.8
COELENTERATA	16			
Velellidae				
Velella velella		5	3.6	0.3
Scyphozoa		11	2.7	0.2
UNIDENTIFIED REMAINS	42.5	1	0.9	<0.1

[a] A single *H. nicans* is included

Hawaiian Archipelago are complex. We found 56 families, 86 genera, and 74 species of fish, and 8 families, 8 genera, and 5 species of squid. We also found an

Table 37. Lengths and volumes of some prey items[a] of the blue-gray noddy. Length and volume values are not necessarily for the same individuals.

Prey	Sample size		Minimum		Maximum		Mean		SE	
	Length	Vol	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)	Length (mm)	Vol (ml)
FISHES										
Blenniidae	10	6	10	<0.1	13	<0.1	12	<0.1	<0.5	0
Exocoetidae	43	8	9	<0.1	39	<0.1	16	<0.1	1	0
Mullidae	24	3	9	<0.1	32	<0.1	18	<0.1	1	0
Synodontidae	36	9	20	<0.1	43	0.4	32	0.2	1	0.1
CRUSTACEA										
Pseudosquilla spp.	34	22	6	<0.1	12	<0.1	9	<0.1	<0.5	0
Coronida spp.	24	14	6	<0.1	12	<0.1	10	<0.1	<0.5	0
Pontella atlantica	29	26	3	<0.1	6	<0.1	5	<0.1	<0.5	0
Shrimps	29	13	6	<0.1	25	<0.1	14	<0.1	1	0
Crab megalopa	46	28	2	<0.1	7	0.3	5	<0.1	0	0
INSECTA										
Halobates sericeus	195	194	2	<0.1	5	<0.1	3	<0.1	0	0

[a] Included are prey items with sufficient measurements in grades 1 and 2 (see Methods).

octopod, 2 gastropod families, an annelid, 11 groups of crustaceans, 2 coelenterates, a tunicate, 3 seabirds, and an alga in the diets (Appendix 3). Plastic particles were found in the stomachs of 4 species, indicating that this potential problem (Baltz and Morejohn 1976, Ohlendorf et al. 1978) is not restricted to northern waters. Nevertheless, it is also evident that relatively few of these prey items comprise most of the food consumed by this seabird community in terms of number, volume, or frequency of occurrence. It is possible that some of the prey items that occur infrequently are necessary to survival in the absence of other food (Ashmole and Ashmole 1967*b*).

For ease of discussion, we have grouped the 18 species into 5 guilds. These are the albatrosses, pelecaniforms, terns and shearwaters associated with predatory fishes, small nocturnal procellariiforms, and neuston feeding terns. These categories are somewhat artificial, and it might be argued that a species could more conveniently be placed in another group. However, we believe this characterization highlights some of the more important similarities and differences among the diets of the seabirds within the tropical and subtropical Hawaiian Archipelago. Each species requires a food source near the surface of the water, and diversification of foraging patterns in such a structurally simple habitat is limited compared to colder waters. We recognize that many differences in prey consumption may be a result of relative rather than absolute prey abundance, but absolute prey abundance data are unavailable. Without such data, it is difficult to assess the "importance" of a prey item. We believe that any prey that ranks high during any season (especially when nestlings are fed) to be important. We acknowledge the probability that some prey rank high simply because they are seasonally abundant. We have no other objective criterion to judge the importance of forage items.

Albatrosses

Albatrosses generally feed well offshore by surface seizing (Ashmole 1971) (Fig. 14). Black-footed and Laysan albatrosses have similar nesting requirements with the exception that black-footed albatrosses nest closer to beaches. Therefore we wished to distinguish between their feeding habits to see if or how they partition food resources. Both species are very dependent on squid (Tables 3 and 6), like other al-

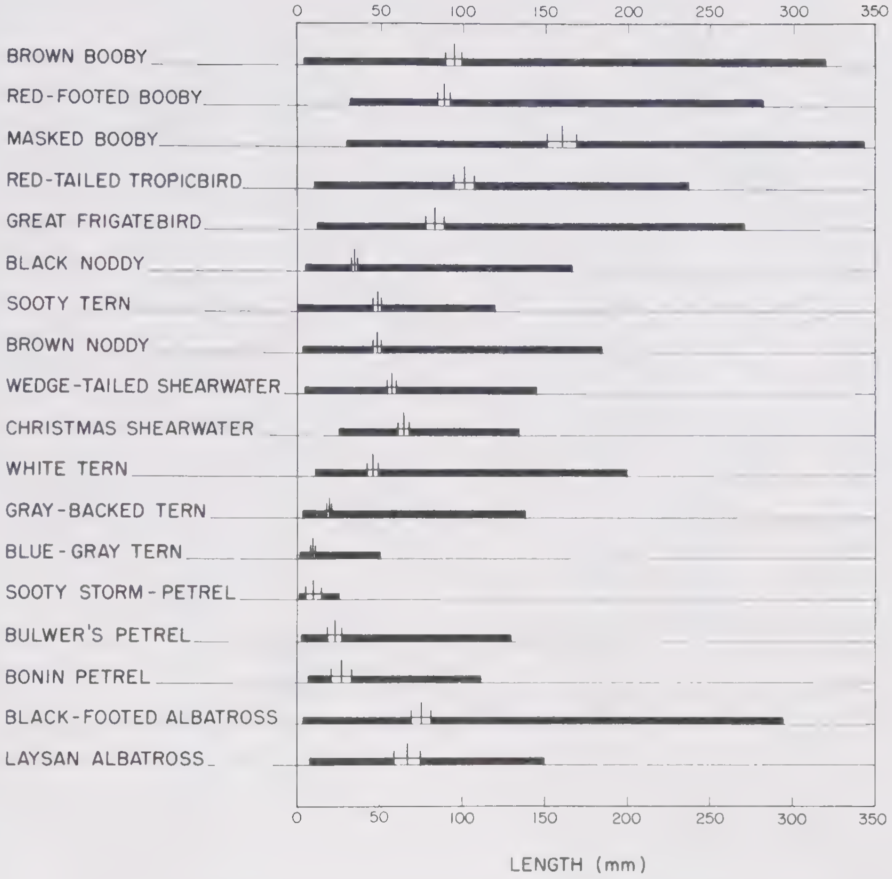

Fig. 13. Comparison of measurable prey lengths for Hawaiian seabirds. Depicted are mean ($\bar{x}$), 95% confidence interval around mean (CI), and range.

batross species (Harris 1973, Imber and Russ 1975). However, Laysan albatrosses consumed by volume far more squid (65%) than black-footed albatrosses (32%). Although it is possible that these birds fed on different species of squid, we could identify to family only 2% of those found in black-footed albatross samples and 6% of those found in the Laysan albatross samples and therefore cannot draw any conclusions. Certainly, ommastrephid squids were commonly eaten by both. A reliable method of identifying the beaks of the species in Hawaii is necessary to determine which squids are most frequently consumed. Fishes were consumed far more by black-footed albatrosses (50% by volume) than Laysan albatrosses (9%). Most of this difference came from the large amount of flyingfish ova in the black-footed albatross diet (44%) compared to that of the Laysan albatross (4%). A comparison of optical density units (D) of rhodopsin in the eyes of these species indicated that Laysan albatrosses are much better adapted for nocturnal vision than are black-footed albatrosses, the former having 16 D/gram and the latter 4 D/gram (A. J. Sillman, pers. commun.). By comparison, pigeons had very little rhodopsin, barn owls had 20 D/gram, and great horned owls had 46 D/gram. An ad-

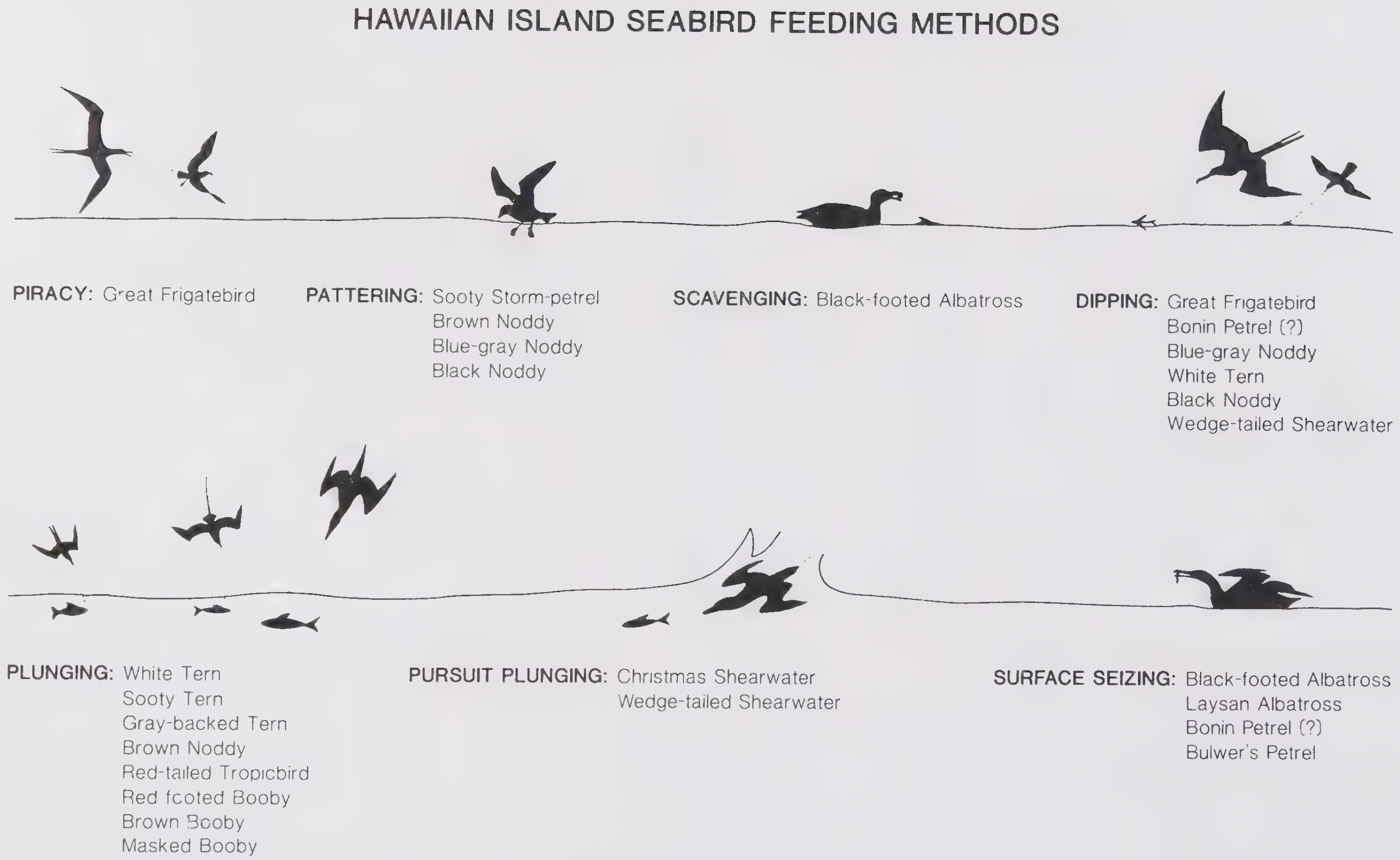

Fig. 14. Seabird feeding methods following Ashmole (1971) and Gould (1971). Used by permission. Drawn by Jon Ahlquist.

aptation for nocturnal feeding explains why Laysan albatrosses took more squid, inasmuch as squid migrate vertically and are more likely to be on the surface during darkness (Clarke 1966). Black-footed albatrosses, by exploiting prey that is more likely to be obtained during daylight hours, ate more flyingfish ova and offal from ships (Miller 1940, Palmer 1962) or dead birds (Table 3). Many of the prey items taken by both species are capable of bioluminescence, which may be important to any predator that feeds at night on vertically migrating prey (Imber 1973). Such items include lanternfishes and hatchetfishes, squids (Onychoteuthidae, Histioteuthidae, Octopodoteuthidae, and Cranchiidae), mysids (*Gnathophausia* spp.), and tunicates (*Pyrosoma* spp.) (Imber 1973). Most importantly, the form of *S. oualaniensis* that occurs in Hawaii has photophores (Young 1975).

There is considerable overlap in the diets of these birds, as evidenced by a comparison of the prey items each consumed, but the proportions of the major items are very different (Tables 2, 6). Feeding at different times of the day may account for much of this difference. Both species feed their young at the same time of the year (Fig. 6), and we detected few differences among seasons in prey consumption in either species. However, Laysan albatrosses exploited Pacific sauries during winter and wind-sailers during spring.

Black-footed albatrosses are heavier and in hand appear to be the stronger, although their bills are shorter than those of Laysan albatrosses (Table 2). The lack of reliable prey measurements and the fact that much of the prey of albatrosses may be shredded before ingestion makes attempts to discuss differences in prey lengths speculative. Laysan albatrosses are much more numerous, outnumbering black-footed albatrosses about 10 to 1 (Table 1).

Pelecaniformes

The 5 species of this order within the study area form a convenient ecological unit for discussion apart from any taxonomic considerations. Each species occurs throughout most of the study area (Table 1), but populations of brown boobies are relatively small. The boobies and tropicbird plunge (Fig. 14) to depths of several meters (Ashmole 1971). Great frigatebirds are limited to snatching prey from surface waters, probably no more than 15 cm in depth, because of a structural inability to take off from the water if they land (R. W. Schreiber, pers. commun.). At sea, frigatebirds often associate with fairly large flocks of other species (Gould 1971). Masked and red-footed boobies are moderately social at sea, feeding in association with small groups of birds. Brown boobies and red-tailed tropicbirds feed in a solitary fashion (Gould 1971). Only brown boobies are thought to feed inshore, the others foraging far at sea (King 1970, Diamond 1978). All species breed in Hawaii during spring and summer, and most dependent young are fed April–September (Fig. 6).

One way in which this guild partitions available prey is in the proportion of fish and squid taken, an observation made on Christmas Island (Pacific) for several of these species by Schreiber and Hensley (1976:247). Red-footed boobies took 27% of their prey volume as squid, the most for any in this group. Red-tailed tropicbirds (18%) and great frigatebirds (14%) took moderate amounts whereas masked boobies (3%) and brown boobies (5%) consumed relatively small amounts. Except for 3 Onychoteuthidae, all identified squids from these species were from the surface-dwelling Ommastrephidae. Flyingfishes were commonly consumed by all species, ranking first for each except for brown boobies, in which they tied for second. Flyingfishes were especially common in the diet of great frigatebirds, accounting for more than 60% of the prey volume (Table 10), a predictable result considering the inability of this species to dive to exploit other fishes. Flyingfishes ranged in percent volume from 58% for masked boobies to 26% for brown boobies. Eight flyingfishes were identified from stomachs of this group (Appendix 3) with *E. voli-*

tans and *Cypselurus* spp. the most frequently identified. Had we been able to identify more of the flyingfishes we may have learned if there were species preferences among the different birds. Carangids, chiefly adult *Decapterus* spp., also were commonly eaten and ranked second or third for each species except brown boobies, where they ranked first. Halfbeaks (especially *Euleptorhamphus viridis*) occurred in the diets of all pelecaniforms but ranked highest in masked and brown boobies. Goatfishes were preyed on by each bird in this guild but ranked high only in the diet of brown boobies (tied for second) and red-footed boobies (fifth). We found little geographical variation in diet, but the ranking of some major prey items changed with season. Flyingfishes and ommastrephid squids generally were taken in substantial quantities throughout the year by each species, but *Decapterus* spp. ranked highest during summer and ranked higher during fall than during spring. Goatfishes ranked highest during spring. Pacific sauries were taken only at Midway during winter where they were commonly eaten by each species except the brown booby. Several birds, at certain seasons and locations, exploited prey species that were not taken by the others. Great frigatebirds took juvenile sooty terns during spring and summer. They ate filefish only in the Laysan Island group during summer. Red-footed boobies took anchovies only on Midway during winter. Red-tailed tropicbirds ate many truncated sun fish on French Frigate Shoals during summer.

Selection of different prey lengths is often considered to be a means of partitioning food resources in the marine environment. Pelecaniforms that weigh more or have longer bill lengths generally take larger prey (Fig. 13). Masked boobies took larger prey than the other 4 species during the spring–summer chick feeding period (Fig. 6) when local food resources probably are most strained. Ommastrephid squids and flyingfishes are likely to be more abundant during spring–summer than fall–winter (Waldron 1964, Akimushkin 1965, Parin 1968, Shuntov 1968, Okutani and Ih-Hsiu 1978). Resource partitioning among the 4 smaller species may occur to some extent by feeding area, e.g., brown boobies feed closer to shore than the others. Feeding methods are also a factor, and the structural differences and behavior may come into play primarily during food shortages when competition would be intensified. Red-tailed tropicbirds, which weigh much less than the other species considered here (Table 2), take prey as large as the other birds. This species has been reported to so seriously misjudge prey length that it can harm itself (Clancy 1974).

The Hawaiian Island pelecaniform community eats organisms similar to those eaten by communities at Christmas Island (Pacific) (Ashmole and Ashmole 1967*b*, Schreiber and Hensley 1976), Ascension Island (Stonehouse 1962, Dorward 1963*a*), and Aldabra Atoll (Diamond 1974*a*,*b*, 1975). Percentages of flyingfishes and squids consumed by each species are similar at Aldabra Atoll and Hawaii. At Christmas Island, however, red-tailed tropicbirds and great frigatebirds ate much larger percentages of squid than in the former locations. The most striking difference was the prevalence of *Decapterus* spp. and goatfishes in the diets of Hawaiian birds. These fishes are rarely eaten elsewhere, and their prevalence here underscores the influence that local availability of surface schooling fishes have on the diets of seabirds in a given location.

Terns and Shearwaters Associated with Predatory Fishes

These 6 species are of fairly similar size, ranging from wedge-tailed shearwaters (388 g) to black noddies (108 g) (Table 2). Other species are the Christmas shearwater, brown noddy, sooty tern, and white tern. Each species fed on similar prey items of similar size and reportedly feeds largely in association with predatory fishes, especially tunas (Ashmole and Ashmole 1967*b*:97). Murphy and Ikehara

(1955:2) found birds so frequently associated with tuna schools in the Central Pacific that they were "virtually inseparable in our observations." At sea these species occur in flocks, with 5 of them associated with other birds between 67% (white tern) and 97% (black noddy) of the time (King 1970). Gould (1971) reported that Christmas shearwaters occurred in flocks in about half of his sightings. These species generally breed throughout the Hawaiian Archipelago, but Christmas shearwaters are restricted in distribution and sooty terns and wedge-tailed shearwaters are especially abundant (Table 1). All species feed most heavily on resources near the islands when young are being fed. This occurs during spring–summer for most species, but wedge-tailed shearwaters feed young during fall and black noddies feed young during winter at some locations (Fig. 13).

This guild feeds using a variety of techniques (Fig. 14). Shearwaters can pursue prey under water whereas terns plunge dive. Sooty terns will plunge dive only to the surface and cause a splash (Gould 1974: 8), yet this species can rarely submerge because it lacks a substantial uropygial gland (Johnston 1979) and cannot get wet without becoming waterlogged. Black noddies feed by pattering on the surface. This guild partitions prey resources in part by selecting different feeding areas. Most of these 6 species feed well offshore, but both black noddies and white terns can feed inshore (Diamond 1978). One of us (CSH) observed black noddies feeding within a few meters of shore at several of the NWHI, often in association with jacks *Caranx* spp. Sooty terns and wedge-tailed shearwaters can feed at night under full moon conditions (Bruyns and Voous 1965, Gould 1967). Christmas shearwaters have a rhodopsin density of 3 D/g, which is not particularly adapted for nocturnal behavior (A. J. Sillman, pers. commun.).

As with pelecaniforms, this guild partitions prey resources by consuming different proportions of fish and squid. The inshore feeding black noddy (92%) and white tern (88%) had diets that were largely fish by volume, with most of the remainder squid. Brown noddies and wedge-tailed shearwaters fed on 66% fish and 33% squid. Christmas shearwaters and sooty terns took half or more of their prey as squid. Except for 4 Onychoteuthidae, all identified squids were Ommastrephidae. These were primarily *S. oualaniensis* but also *H. pelagicus* and *Ommastrephes* spp.

Juvenile goatfishes were consistently the highest ranked prey item in the diets of this guild, ranking first of all prey for 4 species and first among fishes for each. Flyingfishes ranked high but not nearly as high as with the pelecaniforms. Flyingfishes did not rank first in any diet but did rank from second to fifth for each species except wedge-tailed shearwaters. Most identified flyingfishes were *E. volitans* or *Cypselurus* spp. *Decapterus* spp. were relatively common for several birds and ranked second for wedge-tailed shearwaters and fourth or fifth for 3 other species. *Decapterus* spp. was less frequently consumed by the small, inshore feeding white tern and black noddy. Lizardfishes occurred in the diets of each bird but ranked high only in black noddies (second) and brown noddies (third).

We generally found more variation in the diet with season than with location, and some prey items were exploited exclusively in 1 area during 1 season. Ommastrephid squids were taken regularly throughout the archipelago all year by the species that feed on squid. Lizardfishes and flyingfishes were also taken throughout the year, but flyingfishes ranked highest during summer. Goatfishes, the highest ranked family of this guild, were far more prevalent during spring than other seasons but also were common in summer. *Decapterus* spp. were eaten most frequently during summer but also ranked high during spring. Most of the round herrings were taken during spring and summer by terns and noddies, but black noddies ate many at Midway during fall. A filefish (*Pervagor spilosoma*) ranked high in the diet of wedge-tailed shearwaters on Laysan during summer, and lanternfishes were commonly eaten by white terns during spring on Midway.

Prey lengths were fairly similar, but shearwaters generally took larger prey than terns, and black noddies took the smallest prey (Fig. 13). Some stratification or partitioning by prey length clearly takes place, but for several of the most commonly eaten taxa, birds of similar size fed on prey of the same size.

Our results are similar to those at Christmas Island (Ashmole and Ashmole 1967*b*), Ascension Island (Stonehouse 1962, Dorward 1963*b*, Dorward and Ashmole 1963), and Hawaii (Brown 1975). There, ommastrephid squids, flyingfishes, halfbeaks, and tunas are commonly eaten. Hawaiian seabirds generally consumed a smaller proportion of squid than those at Christmas Island. For example, Hawaiian Christmas shearwaters fed on 48% squid compared to 71% on Christmas Island, and white terns fed on 12% squid compared to 50%. In addition, Hawaiian birds ate fewer flyingfishes (although flyingfishes ranked high with several species, especially the white tern) but fed instead on juvenile goatfishes, juvenile lizardfishes, and *Decapterus* spp. Both Christmas Island and Ascension Island birds ate many blennies, which were rarely consumed in Hawaii. Birds at Ascension Island fed on the squid *H. pelagicus*, but those at Christmas Island and the Hawaiian Archipelago fed on *S. oualaniensis*. Size ranges of prey were similar in all areas for which information is available. We conclude that this group of birds is opportunistic in their feeding habits and secures any prey of appropriate size that is available in the surface waters near breeding colonies. Prey for this guild becomes available primarily when it is driven to the surface by predatory fishes, and in the resulting feeding flocks partitioning of prey probably results from differences in feeding technique and morphology. The close association of these birds with tuna schools, especially for foraging, has been reported frequently (Murphy and Ikehara 1955, Ashmole and Ashmole 1967*b*, Gould 1971).

Small Nocturnal Procellariiforms

We consider here the 3 smallest procellariiforms in this seabird community: Bonin petrels, Bulwer's petrels, and sooty storm-petrels. Apparently each feeds extensively at night. Populations of each species occur at several locations in the Hawaiian Archipelago but do not necessarily overlap (Table 1). Sooty storm-petrels and Bonin petrels breed during winter and fledge young in spring, whereas Bulwer's petrels breed during summer (Fig. 6). Bonin petrels are thought to feed by dipping or surface seizing (Fig. 14), but we could not locate definitive observations. Bulwer's petrels feed sitting on the water with wings spread and heads dipped below the surface (Gould 1971:56), and all storm-petrels are strictly surface feeders that feed principally by pattering (Ashmole 1971). Each species feeds offshore in a solitary fashion, occasionally in association with other birds. All have been reported feeding at night (Ashmole 1971, Gould 1971, Crossin 1974). The Bonin petrel has 11 D/g of rhodopsin, which implies some adaptation for nocturnal behavior (A. J. Sillman, pers. commun.).

We acknowledged the difficulties presented by the advanced state of digestion of samples collected from these birds in the species accounts. Bonin and Bulwer's petrels took substantially more fish than squid, whereas sooty storm-petrels took these prey in roughly equal volumes. Most identified fishes from Bonin and Bulwer's petrels were lanternfishes and hatchetfishes, but they also took numerous bristlemouths. These fishes inhabit midwater during daylight, possess photophores, and normally occur on the surface of the ocean only at night or in reduced light conditions (Clarke 1973, Imber 1973). The single fish identified from a sooty storm-petrel was a hatchetfish. Each bird took numerous sea-striders and various crustaceans. Bonin petrels consumed several goatfishes. Flyingfishes were rarely taken, although Bulwer's petrels took enough egg masses from this family for it to rank seventh in its diet. Most of the identified squids were Ommastrephidae, but individual Enoploteuthidae and Histioteuthidae were identified. These families consist largely of individuals with photophores in Hawaii (Imber 1973, Young 1975).

We do not have enough information to draw conclusions concerning seasonal variations in diets among these species or to discuss prey size in detail. Bulwer's and Bonin petrels apparently take somewhat larger prey than sooty storm-petrels. Bonin and Bulwer's petrels breed at sufficiently staggered seasons that competition for prey in the vicinity of the breeding islands probably is avoided (Fig. 6). Bonin petrels ate relatively more fish than squid compared to other *Pterodroma* spp. (Ashmole and Ashmole 1967*b*, Imber 1973) but were similar in feeding on mesopelagic fishes and sea-striders. The taking of hatchetfishes, sea-striders, and by-the-wind sailors by sooty storm-petrels is consistent with studies indicating that storm-petrels feed on surface organisms (Crossin 1974). Our conclusion that these species feed to a large extent at night does not preclude the probability that daylight feeding also occurs. Lanternfish occur on the surface of the sea during daylight hours when chased there by yellowfin or skipjack tunas (Alverson 1961). Fresh lanternfish were taken by one of us (CSH) from a white tern chick that had just been fed by a marked adult at 1000 and 1100 hours on Midway Island. The heavy reliance by Bonin and Bulwer's petrels on midwater fishes makes it probable that nocturnal feeding accounts for much of their diets.

Neuston Feeding Terns

We treat gray-backed terns and blue-gray noddies as a guild because their unique feeding habits do not conveniently fit elsewhere and because they have some similarities in their diets. Both are thought to feed inshore (Diamond 1978), and both took small prey (Fig. 13). Gould (1971) stated that gray-backed terns are gregarious and feed by plunging in flocks with other species, but his data are limited (29 sightings). The lack of sightings at sea may be due to the fact that from a distance gray-backed terns can be mistaken for the more numerous sooty terns. Blue-gray noddies feed by dipping and pattering at the surface (Fig. 14) and seemingly are not dependent on schools of predatory fishes to drive prey to the surface. Gray-backed terns breed at most of the islands in the Hawaiian Archipelago, but blue-gray noddies are restricted to the southern portion (Table 1). Blue-gray noddies feed most of their young during late winter and spring whereas gray-backed terns feed most chicks during spring and early summer (Fig. 6).

Neither of these species ate much squid, gray-backed terns taking 4% by volume and blue-gray noddies 1.5%. The tern ate 92% fish whereas the noddy took only 61%, eating instead crustaceans (copepods and stomatopods) (18%) and sea-striders (18%). Blue-gray noddies are the most important avian predator on sea-striders in the NWHI (Cheng and Harrison 1983). Gray-backed terns ate many cow fish (42%), a prey item rarely taken by other birds. Blue-gray noddies also took some cowfish, and gray-backed terns also ate sea-striders. Both birds ate juvenile flyingfishes and goatfishes. Gray-backed terns also ate many dolphin-fishes and round herrings, whereas blue-gray noddies supplemented their diet with larval lizardfishes. Hence, these species fed on many taxa common to those taken by other seabirds in this community. The reliance of gray-backed terns on cow fish and blue-gray noddies on minute prey such as sea-striders, copepods, and stomatopods is unique.

We have no information on the absolute abundance of prey species. However, goatfishes ranked highest for both species during spring. Sea-striders were consumed more frequently during spring than winter, and dolphin-fishes were eaten primarily during spring and summer. Gray-backed terns are larger than blue-gray noddies (Table 2) and took larger prey.

The diet of blue-gray noddies at Christmas Island (Pacific) is very similar (Ashmole and Ashmole 1967*b*). There, as in Hawaii, they fed largely on sea-striders and crustaceans, in sharp contrast to other species. At both locations flyingfishes ranked high and prey was minute, with fish having mean volumes of about 0.1 ml. Hawaiian birds fed heavily on lizardfishes and goatfishes, which were absent in the diet at Christmas Island. Christmas Island birds fed largely on snake mackerels, tunas, and blennies, which were present but did not rank very high in the diet of Hawaiian birds. Blue-gray noddies occupy the same trophic level and have similar diets in each location. Differences in their diets probably result primarily from differences in prey species in waters adjacent to study islands.

Timing of Breeding Season and Food Availability

It is well understood that breeding season for marine birds is related to the food supply in temperate and cold waters (Belopol'skii 1957, Pearson 1968, Bedard 1969, Croxall and Prince 1980). Breeding seasons in tropical waters are less predictable (Harris 1969, Schreiber and Ashmole 1970), in part because birds in moderate climates do not face the ecological imperatives encountered in cold water regions. The modal breeding season of Hawaiian seabirds is predictable (Fig. 6) even though (1) year to year variations may change egg-laying dates by many weeks, (2) breeding of terns and pelecaniforms is generally protracted, and (3) a few individual birds of most species may be found in any stage of the breeding cycle for much of the year (Richardson 1957).

Why is the breeding season of the Hawaiian seabird community more predictable than that of others comprising similar species? One consideration in determining why this community displays the spring–summer breeding season found in more northern marine bird communities is its location. Much of the Hawaiian Archipelago is subtropical and is at the northern extent of the breeding ranges for many of its tropical bird species; Kure is the northernmost coral atoll on earth (Woodward 1972). Peak food availability often has been suggested as a controlling factor in the timing of seabird breeding. Pearson (1968:527) found the breeding of the seabirds in Scotland to coincide "with the period of greatest abundance of the Ammodytidae and Clupeidae in the area." Harris (1969:151) found in the Galapagos that unpredictable food shortages were closely related to breeding success for the Audubon shearwater and concluded that food supply is "the proximate factor controlling breeding." The chick feeding interval is generally much less than the incubation shift with tropical marine birds (Diamond 1978:218, Harrison and Hida 1980:27). This phenomenon implies that during the chick feeding period (Fig. 14) the local waters near the breeding islands must provide most of this food. Ashmole (1963*a*:464) stated that high latitudes have an enormous flush of food in spring, but in "tropical oceans seasonal fluctuations in food abundance are generally much less extreme." It was beyond the scope of our investigation to measure seasonal or annual levels of major prey resources, but we recognize that such information would be useful in interpreting these data.

Juvenile goatfishes were the most commonly eaten prey item for the guild that associates with tunas. Goatfishes spawn during spring–summer in Hawaii (Miller 1974), and juvenile goatfishes are not abundant during fall and winter. Akimushkin (1965:184) stated that squids generally migrate with season, especially shoreward to deposit eggs. The biology of ommastrephid squids in Hawaii is insufficiently known to be sure whether they have predictable breeding seasons or migrations (R. E. Young, pers. commun.). The distribution of flyingfishes indicates that they vary in abundance with water temperature (Parin 1963, 1968; Shuntov 1968). Shuntov (1968:784) found that "flyingfishes were found singly when surface water temperature was 19–20 C, were practically a common occurrence at 23–25 C, and were very sharply increased in numbers in areas where the water was above 25 C." The surface isotherms for the Hawaiian Archipelago (Fig. 1) indicate that flyingfishes are far more common during spring–summer than winter. *Decapterus* spp. spawn during spring–summer (Yamaguchi 1953) as do dolphinfishes (Mito 1960). Consequently, juveniles of these fishes would not be abundant during fall and winter. Adult *Decapterus* spp. are resident but may become more available during summer when chased to the surface by migratory tunas, which are usually far more numerous during spring–summer than winter (Waldron 1964). The presence of tunas or other predatory fishes is apparently essential to enable many species to obtain prey (Ashmole and Ashmole 1967*b*:97). The biology of sea-striders is insufficiently known to determine if or when they have a breeding season (Cheng 1973, 1974), but they are known to be most abundant in 24–28 C water (Cheng and Shulenberger 1980). Winter temperatures in the Hawaiian Archipelago (Fig. 1) are at or below the lower end of this range.

The majority of young of most bird species are fed during spring–summer (Fig. 6), and the increased availability of food resources during this time is the best explanation for the observed breeding season. We do not contend that prey is altogether unavailable in winter; indeed we found some flyingfishes, ommastrephid squids, and lizardfishes throughout the year. However, the surge in available prey during spring–summer because of spawning activities (e.g., goatfishes, *Decapterus* spp.) and tuna migration is a controlling factor for the regular spring–summer breeding seasons. Tropical birds that feed by daylight have less time each day to search for food than their northern counterparts and need the relative certainty of encountering prey near the breeding colonies during spring–summer to reproduce. Several bird species are migratory, abandoning breeding colonies during winter months to forage elsewhere, an adaptation argued by Diamond (1978:222) to be "rewarded by greater population size with its attendant diminution of the risk of extinction."

Five of the 18 species in this community feed their young during winter (Fig. 14). Laysan albatrosses, Bonin petrels, and sooty storm-petrels all feed nocturnally and thereby exploit different prey than summer breeders that feed by day. The ability to breed during winter is enhanced by decreased day length because this allows more time to forage. Black-footed albatrosses exploit a unique resource, flyingfish eggs, that may be available only in winter–spring. In addition, both albatrosses fly much further from the nesting site than other species, especially during incubation (Harrison and Hida 1980) and may be less dependent on local food resources because they can forage over a larger area. It is likely that Bonin petrels and sooty storm-petrels are forced to breed during winter because of competition for nest sites by the larger wedge-tailed shearwaters and Bulwer's petrels. Wedge-tailed shearwaters arriving on Laysan in spring kill juvenile Bonin petrels and sooty storm-petrels and cast them from their burrows (M. B. Naughton, pers. commun.). Black noddies have the least predictable breeding season of any Hawaiian seabird. They feed in association with inshore predatory fishes (*Caranx* spp.) that drive prey to the surface, enabling young to be raised during winter because these fishes are resident.

An alternative hypothesis is that breeding during winter months is inefficient because of weather. Winter temperatures are much cooler than summer, and storms are frequent in the Hawaiian Archipelago. Black noddy colonies at French Frigate Shoals have been decimated in winter by high winds blowing nests from heliotrope shrubs (*Tournefortia argentea*) and hundreds of black-footed albatross chicks have been drowned by storm tides (R. P. Schulmeister, pers. commun.). This is another relevant factor that explains why this seabird community breeds during spring–summer, but we believe that food availability is much more important. The fact that even small species such as sooty storm-petrels and black noddies can fledge young in a winter breeding cycle is evidence against weather being a limiting factor.

Opportunistic Feeding and Diet Diversity

Seabirds in Hawaii feed on a wide variety of shoaling fish and squid and apparently take anything of appropriate size that occurs in surface waters. This diversity is reflected in the fact that no bird ate any 1 prey species to an extent that it comprised half or more of the volume of the diet. Our analysis is confounded by prey material that could not be identified to species, but even the highest ranking prey family for many birds was relatively low by volume: brown booby (15%), wedge-tailed shearwater (18%), white tern (20%), brown noddy (28%), and black noddy (31%). Diets that contain 20–40 prey families are very diverse compared to those in northern latitudes (Pearson 1968). The most specialized diets were those of gray-backed terns (42% cowfish) and black-footed albatrosses (44% flyingfish eggs), but the latter included more than 1 species. Percentage volumes are higher for unidentified flyingfishes and unidentified squids for Laysan albatrosses and some pelecaniforms, but these categories include many prey species and it is unlikely that any one accounts for as much as half of the prey. In contrast, seabirds in Peru feed 80–96% on a single fish (Jordan 1959, 1967).

The opportunistic character of these feeding strategies is evidenced by the many prey items that were taken only during 1 season or at 1 location. Many prey taxa were taken only seasonally, probably reflecting seasonal occurrence in surface waters. We are limited by an inability to distinguish between relative and absolute prey abundance. Much of the variation in diet occurs in the relative proportions of several common prey families.

The most numerous birds in this community are those that eat many squid (compare Laysan and black-footed albatrosses; red-footed, masked, and brown boobies; sooty and gray-backed terns; brown and black noddies). These population differences may be merely another expression of the proposition that pelagic feeders are more numerous than inshore feeders (Diamond 1978). Without data on the availability of prey, we cannot know whether food directly controls population size. Inshore feeding species seem to have more diverse diets than offshore feeding ones. It is tempting to attribute this difference to enhanced competition in inshore feeding areas, but inshore fauna is much more diverse than pelagic fauna.

Differences in feeding zones and feeding locations are used to explain differences in diets, often without convincing evidence (Ashmole and Ashmole 1967*b*, Pearson 1968) and are based on inferences from incubation shifts, chick feeding frequencies, or scattered observations at sea in the vicinity of the colony without means to distinguish breeding from nonbreeding birds. Ashmole and Ashmole (1967*b*:63) analyzed feeding zonation using percentages of fish that belonged to pelagic and reef-originating families. This analysis is useful but is limited by the fact that epipelagic species such as flyingfishes and halfbeaks regularly occur in shallow water in the NWHI. As Diamond (1974*b*:208) pointed out, the pelagic-feeding red-footed booby on Aladabra Atoll could feed over water 500 m deep at 1 km from the reef, a situation common in the Hawaiian Archipelago. Future investigators must locate feeding areas of tropical seabirds to determine the importance of feeding zones and to protect them from marine development. Radiotelemetry (Harrison and Stoneburner 1981) is a useful technique in this endeavor. The notion that most tropical birds feed far offshore must be challenged if we are to further our understanding of the forces that shape their feeding and breeding ecology

CONCLUSIONS

1. Seabirds in Hawaii are opportunistic and feed on any prey of appropriate size that occurs in surface waters.
2. Similar to other tropical communities,

Hawaiian seabirds consume many flyingfishes and ommastrephid squids. This community is distinguished by the occurrence in the diets of many juvenile goatfishes, juvenile lizardfishes, *Decapterus* spp., and mesopelagic fishes.

3. Compared to Christmas Island, seabirds in Hawaii consume more fish than squid.
4. Variation in diets is more correlated with season than with location. However, during certain months at Midway, prey species such as Pacific sauries and round herrings are taken that do not occur elsewhere.
5. The time of year during which most young are fed (spring–summer) is correlated with the maximum availability of prey.
6. Larger predators took larger prey than smaller predators, but during spring–summer, similar-sized birds had few significant differences among lengths of common prey items.
7. Diets provide circumstantial evidence that Laysan albatrosses, Bonin petrels, Bulwer's petrels, and sooty storm-petrels feed at night.
8. Many fundamental questions concerning the biology of tropical and subtropical seabirds cannot be answered until better methods of measuring the availability of prey are developed.

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APPENDIXES

Appendix 1. Common and scientific names of birds.

Common name	Scientific name
Barn owl	*Tyto alba*
Black-footed albatross	*Diomedea nigripes*
Black noddy	*Anous minutus (tenuirostris)*
Blue-gray noddy	*Procelsterna cerulea*
Bonin petrel	*Pterodroma hypoleuca*
Brown booby	*Sula leucogaster*
Brown noddy	*Anous stolidus*
Bulwer's petrel	*Bulweria bulwerii*
Christmas shearwater	*Puffinus nativitatis*
Gray-backed tern	*Sterna lunata*
Gray-faced petrel	*Pterodroma macroptera gouldi*
Great frigatebird	*Fregata minor*
Great horned owl	*Bubo virginianus*
Laysan albatross	*Diomedea immutabilis*
Masked booby	*Sula dactylatra*
Phoenix petrel	*Pterodroma alba*
Red-footed booby	*Sula sula*
Red-tailed tropicbird	*Phaethon rubricauda*
Rock dove	*Columbia livia*
Sooty storm-petrel	*Oceanodroma tristrami*
Sooty tern	*Sterna fuscata*
Wedge-tailed shearwater	*Puffinus pacificus*
White tern (fairy tern)	*Gygis alba*

Appendix 2. Common and scientific names for frequently consumed prey.

Common name	Scientific name
Amberjack	*Seriola* spp.
Anchovy	*Stolephorus buccaneeri*
Balloon fish	*Lagocephalus lagocephalus*
Blenny	Blenniidae
Bristlemouth	*Gonorhynchus gonorhynchus*
Cowfish	*Lactoria fornasini*
Dolphin-fish	*Coryphaena* spp.
Filefish	Monacanthidae
Flying fish	Exocoetidae
Flying gurnard	*Dactyloptena orientalis*
Goatfish	Mullidae
Goby	*Ptereleotris heteropterus*
Halfbeak	Hemiramphidae
Hatchetfish	Sternoptychidae
Lanternfish	Myctophidae
Lizardfish	Synodontidae
Man-o-war fish	*Nomeus gronovii*
Marlin	Istiophoridae
Mantis shrimp	Stomatopoda
Needlefish	Belonidae
Pacific saury	*Cololabis saira*
Pilot fish	*Naucrates ductor*
Round herring	*Spratelloides delicatulus*
Rudderfish	*Kyphosus bigibbus*
Sea-strider	*Halobates sericeus*
Silverside	*Pranesus insularum*
Skipjack tuna	*Katsuwonus pelamis*
Snake mackerel	*Gempylus serpens*
Squirrelfish	Holocentridae
Striped hawkfish	*Cheilodactylus vittatus*
Truncated sun fish	*Ranzania laevis*
By-the-wind sailor	*Velella velella*

Appendix 3. List of occurrence of prey items by bird species: white tern (WHTE), black noddy (BLNO), brown noddy (BRNO), blue-gray noddy (BGNO), gray-backed tern (GBTE), sooty tern (SOTE), great frigatebird (GRFR), brown booby (BRBO), red-footed booby (RFBO), masked booby (MABO), red-tailed tropicbird (RTTB), sooty storm-petrel (SSPE), Bulwer's petrel (BUPE), Bonin petrel (BOPE), Christmas shearwater (CHSH), wedge-tailed shearwater (WTSH), Laysan albatross (LAAL), and black-footed albatross (BFAL). A plus (+) designates occurrence and an asterisk (*) designates an item especially important in dietary ranking.

	WHTE	BLNO	BRNO	BGNO	GBTE	SOTE	GRFR	BRBO	RFBO	MABO	RTTB	SSPE	BUPE	BOPE	CHSH	WTSH	LAAL	BFAL
FISHES																		
Ammodytidae																		
Bleekeria gillii		+	+		+	+		+	+		+				+	+		
Atherinidae																		
Pranesus insularum	*	+			+	+	+	+										
Balistidae		+		+	+		+											
Xanthichthys mento					+													
Belonidae	+				+					+	+							
Platybelone argulus platyura		+						+		+								
Ablennes hians	*	+		+	+	+		+	+	+	+							
Blenniidae	+	+	+	+	+	+		+						+				
Plagiotremus goslinei	+																	
Bothidae		+	+	+														
Bothid larvae				+														
Bramidae																		
Brama orcini					+		+											
Pteraclis velifer	+		+		+	+												
Canthigasteridae																		
Canthigaster sp.	+																	
Carangidae	+	+	+		+	+		+	+					+	+	+		
Decapterus spp.	+	+	*		+	+	*	*	*	*	*				*	*		+
D. macarellus								+	+	+								
D. macrosoma	+	+	+		+	+	*	*	+	*	+		+		+	*		
D. tabl		+	+			+	+	+	+		+					+		
Selar crumenophthalmus			+				+	+								+		
Naucrates ductor	+	+	+	+	+	+		+			+							
Seriola spp.	+		+	+	+			+	+							+		
Caranx spp.	+							+										
Carangoides ferdau					+													
Chaetodontidae			+															
Chaetodon sp.	+																	
Chaunacidae					+													
Cheilodactylidae																		
Cheilodactylus vittatus	+	+	+		+	+			+									
Cirrhitidae		+				+												
Cirrhitops fasciatus			+							+								
Clupeidae																		
Spratelloides delicatulus	+	*	+		*	+												
Sardinella marquesensis																+		
Congridae					+									+				
Coryphaenidae																		
Coryphaena spp.	+	+		+	+		+	+	+	+	+					+		
C. hippurus	+	+		+	*	+	+	+	+	+	+				+			
C. equiselis	*	+	+		+		+	+	+	+	+				+	+		
Dactylopteridae																		
Dactyloptena orientalis		+		+	+	+	+								+	+		
Diodontidae	+			+	+				+		+							
Diodon spp.	+			+	+						+							
D. hystrix											+							
Echeneidae	+					+		+		+	+							
Remora spp.	+			+														
R. remora		+																
Remoropsis brachypterus								+			+							
Rhombochirus osteochir	+	+		+	+													
Eleotridae																		
Asterropteryx sp.				+														
Engraulidae																		
Stolephorus buccaneeri	+	+	+						+							+		

Appendix 3. Continued.

	WHTE	BLNO	BRNO	BGNO	GBTE	SOTE	GRFR	BRBO	RFBO	MABO	RTTB	SSPE	BUPE	BOPE	CHSH	WTSH	LAAL	BFAL
Exocoetidae	*	*	*	*	*	*	*	*	*	*	*		+	+	*	*	+	+
Exocoetus sp.								+										
E. volitans	+	+	+			+	*	*	*	*	*		+		+			
E. monocirrhus	+				+			+										
Prognichthys gilberti	+	+			+			+										
Cypselurus spp.	*	+	+	+	+	+	*	+	*	*	+						+	
C. speculiger	+						+	+	+	+	+							
C. simus							+											
C. spilonotopterus								+										
C. atrisignis	+	+						+	+	+								
C. spilopterus							+		+		+							
Exocoetidae ova													+				*	*
Fistulariidae			+													+		
Gempylidae	+	+	+	+		+		+	+		+			+			+	+
Gempylus serpens	+	*	*	+	+	*	+	+	+	+	+			+	+	+		
Gobiidae		+		+														
Ptereleotris heteropterus		*	+	+												+		
Gonorhynchidae																		
Gonorhynchus gonorhynchus	+	+	+	+	+				+						+			
Gonostomatidae																		
Vinciguerria spp.			+			+			+				+	+	+	+	+	
V. nimbaria					+	+			+				+	+				
Diplophos sp.													+					
Hemiramphidae	+	+	+	+			+	+	+	+	+						+	
Euleptorhamphus viridis	+	+		+			+	*	+	*	+						+	
Hyporhamphus acutus pacificus	+			+				+										
Oxyporhamphus micropterus	+	+			+	+	+	+	+						+			
Holocentridae	+	+	+	+	+	+			+					+	*	+		
Neoniphon sammara			+															
Sargocentron spp.		+	+			+			+									
Holocentrid larvae		+																
Myripristis chryseres	+																	
Hoplichthydae																		
Hoplichthys sp.	+																	
Istiophoridae		+	+	+	+				+	+	+				+			
Istiophorus platypterus	+				+													
Tetrapterus angustirostris					+		+			+								
Makaira nigricans	+	+	+	+	+													
Istiophorus spp.				+														
Kyphosidae																		
Kyphosus bigibbus		+	+		+		+	*	+	+	+					+		
Labridae																		
Hemipteronotus leclusei								+										
Macrorhamphosidae																		
Macrorhamphosus gracilis	+	+	+	+	+	+			+						+			
Macrouridae					+		+											
Molidae																	+	
Ranzania laevis		+	+			+	+		+		*						+	
Masturus lanceolatus							+		+		+							
Monacanthidae			+		+	+	+		+		+			+	+	*		
Pervagor spilosoma		+	+		+	+	+									+		
Alutera scripta					+													
Cantherhines spp.	+					+												
C. verecundus						+												
Mugilidae	+	+			+													
Mullidae	*	*	*	*	*	*	+	*	*	+	+			*	*	*	+	
Myctophidae	+	+	+		+	+			+		+		*	*		+	+	
Benthosema fibulatum	+																	
Hygophum spp.													+	+				
Myctophum spp.													+	+				
Lampanyctus spp.													+					
Diaphus spp													+					
Symbolophorus sp													+					

Appendix 3. Continued.

	WHTE	BLNO	BRNO	BGNO	GBTE	SOTE	GRFR	BRBO	RFBO	MABO	RTTB	SSPE	BUPE	BOPE	CHSH	WTSH	LAAL	BFAL
Nomeidae	+	+	+	+	+	*	+	+	+		+		+		+	+		
Nomeus gronovii	+	+		+	+	+		+										
Psenes sp.																+		
P. cyanophrys		+			+			+	+	+								
Cubiceps pauciradiatus											+							
Opisthoproctidae																		
Opisthoproctus sp.													+					
Ostraciontidae				+														
Lactoria fornasini				+	*		+											
Pegasidae																		
Pegasus papilio					*													
Polymixiidae																		
Polymixia japonica							+											
Pomacentridae	+	+	+	+	+	+				+	+							
Chromis sp.		+																
C. vanderbilti	+																	
C. struhsakeri	+																	
Priacanthidae					+		+	+	+							+		
Priacanthus spp.								+			+							
P. cruentatus							+											
Scomberesocidae				+														
Cololabis saira		+	+				+	+	*	+	+						+	
C. saira (ova)																	+	
Scombridae		+	+	+		+	+	+	+		+							
Scomber japonicus								+										
Auxis spp.							+				+							
A. thazard										+								
Katsuwonus pelamis	+	+	+		+	+	+	+	+	+	+				+	+		
Thunnus spp.						+			+									
T. alalunga		+	+				+											
Acanthocybium solandri								+										
Unidentified tuna	+	+			+													
Scombrid larvae		+																
Tuna larvae		+		+														
Serranidae																		
Grammatonotus laysanus	+																	
Odontanthias elizabethae					+													
Soleidae	+			+	+													
Aseraggodes kobensis					+													
Sphyraenidae		+	+	+	+				+									
Sphyraena helleri			+					+										
Sternoptychidae		+			+							+	*	*	+			+
Sternoptyx diaphana					+													
Argyropelecus sp.													*	+			+	
Synodontidae	+	*	*	*	+	+			+		+			+	+	+		
Synodus sp.	+																	
Trachinocephalus myops				+														
Tetraodontidae	+		+		+		+				+					+		
Lagocephalus lagocephalus		+	+		+		+		+		+							
Xiphiidae																		
Xiphias gladius	+			+	+	+	+				+							
Unidentified fishes	*	*	+	*	*	*	*	+	+	+	*	*	*	*	*	*	*	*
Unidentified fish larvae	+	+		*	+													
Unidentified fish juvenile		+		+														
Leptocephalus larvae		+	+	+												+		
Anguilliformes		+																
Pleuronectoidei (flatfish)		+											+	+				
Tetrodontoidei (puffer)											+							
MOLLUSCA																		
Decapoda (squid)	+	+	*	+	+	*	*	+	*	+	*	*	*	*	*	*	*	*
Ommastrephidae	*	*	*	+	+	*	+	*	*	*	*		+	+	*	*	*	*
Ommastrephes spp.			+			+		+	+		+							

Appendix 3. Continued.

	WHTE	BLNO	BRNO	BGNO	GBTE	SOTE	GRFR	BRBO	RFBO	MABO	RTTB	SSPE	BLPE	BOPE	CHSH	WTSH	LAAL	BFAL
Symplectoteuthis spp.	+	+	*		+	*	+	+	+	+	+				*	+	+	
S. oualanienis	+	+	+			+	+	+	+	+	+				+	+	+	+
S. luminosa			+				+	+	+									
Hyaloteuthis pelagicus	+					+			+	+	+				+	+		+
Cranchiidae																		+
Lepidoteuthidae																	+	
Mastigoteuthidae																		
Mastigoteuthis sp.																	+	
Enoploteuthidae																		
Thelidioteuthis alessandrinii																	+	
Pterygioteuthis microlampas														+				
Onychoteuthidae											+				+		+	
Onychoteuthis spp.			+								+							
Onykia spp.		+																
Histioteuthidae														+			+	
Octopoteuthidae																		+
Octopoda																+		+
Gastropoda													+					
Janthinidae																		
Janthina spp.					+													
J. pallida					+													
J. pallida (egg masses)																	+	
J. prolongata					+													
Cavolinidae																		
Cavolinia tridentata					+													
ANNELLIDA																		
Polychaeta													+					
ARTHROPODA																		
Crustacea (unidentified)												+	+	*		+	*	*
Crustacean larvae				+									+		+	+		
Mysidacea				+										+			+	+
Lophogastridae																		
Gnathophausia spp.														+			+	+
G. gigas																	+	+
G. ingens																	+	+
Mysidae																		
Siriella spp.				+														
Euphausiacea			+	+	+							+		+			+	+
Stomatopoda		+		+							+							
Stomatopod larvae		+		+														
Squillidae																		
Pseudosquilla spp.		+		+													+	
Squilla spp.		+		+														
Lysiosquilla spp.		+	+	+							+					+		
Coronida spp.		+		+														
Odontodactylus spp.			+	+														
O. brevirostris			+															
Amphipoda				+								+	+	+			+	+
Oxycephalidae														+				
Eurythenes gryllus																	+	
Alicella sp.																		+
Isopoda				+	+			+				+					+	+
Cymothoidae																		
Anuropus spp.														+			+	+
A. branchiatus																	+	+
Parasitic Isopoda				+	+									+		+	+	+
Nebaliacea																		
Nebaliidae																		
Nebaliopsis typica																	+	+
Copepoda				+									+	+				
Pennellidae																		
Penella spp.									+									+

Appendix 3. Continued.

	WHTE	BLNO	BRNO	BCNO	GBTE	SOTE	GRFR	BRBO	RFBO	MABO	RTTB	SSPE	BUPE	BOPE	CHSH	WTSH	LAAL	BFAL
Pontellidae				+														
Pontella spp.				+														
P. atlantica				*	+													
Calanoid copepod				+										+				
Parasitic copepod														+				
Decapoda																		
Shrimp		+		+	+	+					+	+	+	+			+	+
Penaeidea	+	+																
Penaeus marginatus		+																
Gennadus sp.	+																	
Aristaeinae		+																
Caridea		+															+	
Oplophoridae																	+	+
Notostomus spp.																	+	+
N. japonicus																		+
Acanthephyra sp.																	+	
A. eximia																	+	
Sergestidae				+														
Lucifer spp.				+														
Pasiphaeidae																	+	+
Crab (Brachyura)					+											+	+	+
Crab megalopa		+		*	*								+	+		+		
Portunidae					+													
Galatheidae														+				
Grapsidae																		
Planes cyaneus					+												+	+
Insecta									+									
Gerridae																		
Halobates sericeus			+	*	+							+	*	*		+	+	+
H. micans				+														
Lepidoptera (moth)					+													
Caterpillar		+										+						+
Orthoptera (grasshopper)																		
Euconocephalus nasutus					+													
Argasidae (tick)																		
Ornithodorus capensis												+						
COLENTERATA																	+	
Velellidae																		
Velella velella				+	+	+						*					*	+
Scyphozoa				+		+										+		
TUNICATA																		
Pyrosomatidae														+			+	+
BIRDS																		
Procellariiformes																		
Puffinus sp.																		+
P. pacifucus																		+
Pterodroma hypoleuca																		+
Laridae																		
Sterna fuscata							+											
ALGAE																		
Fucaceae																		
Sargassum sp.																		+
UNIDENTIFIED REMAINS		+	+	+	+		+		+	+	+	+	*	*	+	+	*	*
UNIDENTIFIED MEAT							+											+

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ROLL, HEAVE AND VERTICAL ICHTHYOPLANKTON TOWS

Roger Hewitt

National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038

ABSTRACT

A simple model of ship's motion is described and used in the design of vertical ichthyoplanktons tows. The velocity of the net, as it is affected by roll, heave and retrieval rate, is plotted for the duration of the tow. After simulating various conditions the retrieval rate may be specified that minimizes extrusion of soft bodied organisms and is still sufficient to prevent stalling and back flushing of the net; the model may also be used to specify the sea state at which field operations should be suspended.

INTRODUCTION

The CalCOFI (California Cooperative Oceanic Fisheries Investigation) Vertical Egg Tow (CalVET) was designed to collect pelagic fish eggs occurring from 70 m depth to the surface. Design specifications included a 0.05 m^2 net aperture, 0.87 m^2 filtering surface and .333 mm nylon mesh net. Operational specifications dictated that the net be deployed at 70 m/min, allowed to rest at depth for 10 sec, and retrieved vertically at 70 m/min. (Figure 1).

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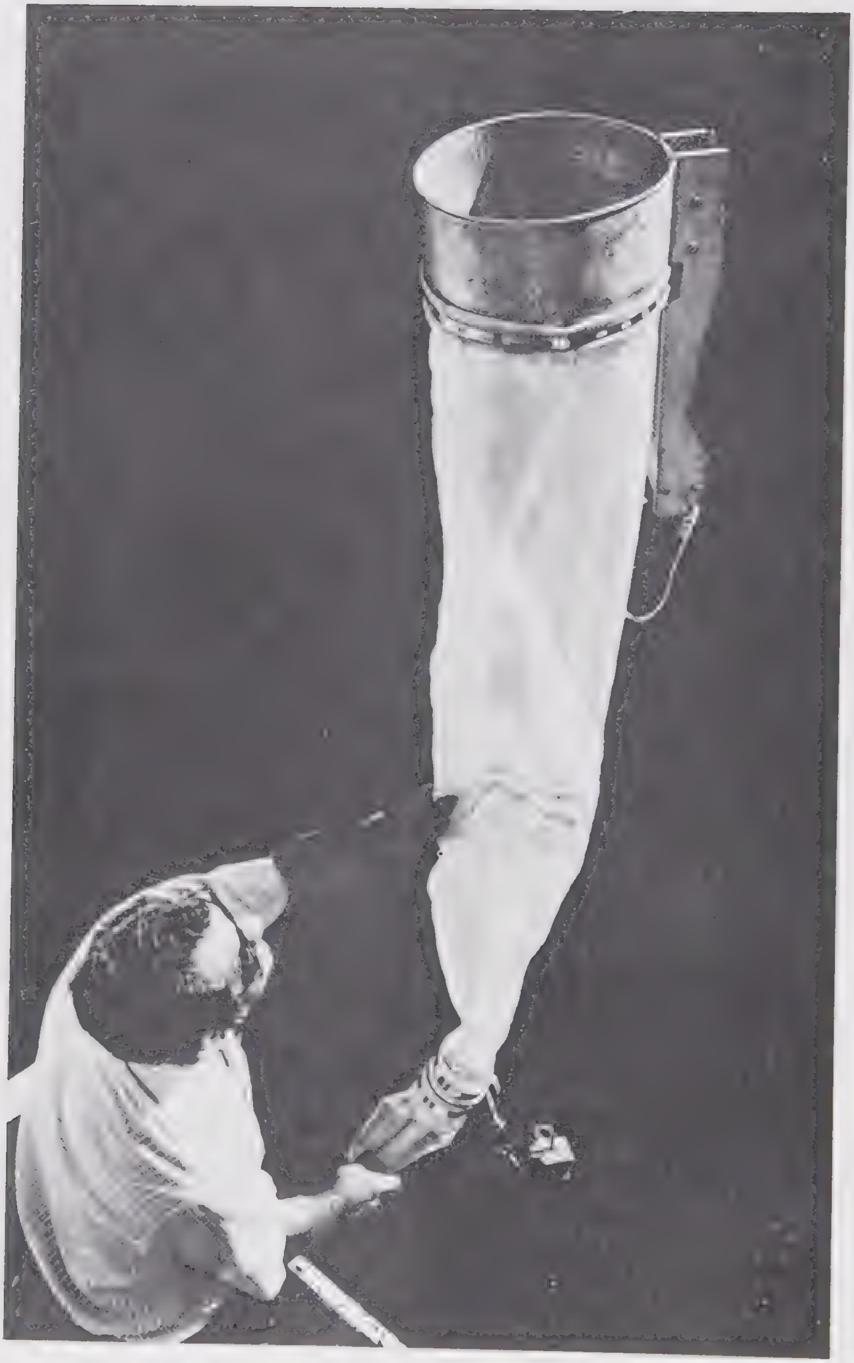


FIG. 1. The CalVET net is retrieved vertically from 70 m depth and is designed to sample pelagic marine fish eggs. Fish abundance is determined by relating egg production to adult fecundity.

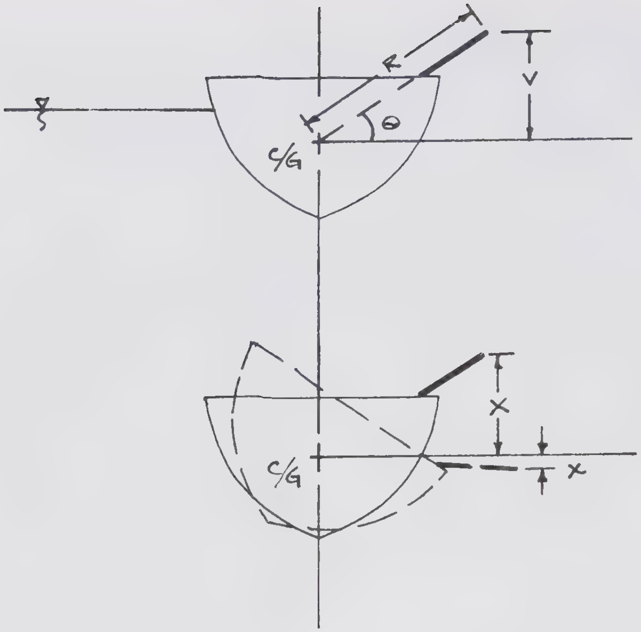
The retrieval rate specified was a compromise between the desire to minimize extrusion of soft bodied organisms through the meshes of the net and the necessity to overcome the downward velocity caused by the ships roll. As the ship rolls, in response to surface waves, the end of the winch boom traverses a vertical arc. If the downward velocity of the boom exceeds the upward velocity of the net frame then the net will collapse and its contents will be "pumped" out. The upward velocity of the end of the winch boom adds to the retrieval velocity and thus aggrevates the extrusion problem. To minimize losses caused by extrusion and pumping the retrieval rate should be just great enough to overcome stalling caused by the ship's roll.

The specified retrieval rate of 70 m/min was an initial estimate of the optimum rate. The present study refines the estimate of optimum retrieval rate by using an analytical description of ship's motion. Given the ships design characteristics and the sea state, the optimum retrieval rate is specified; a rate which will minimize the loss of material caused by extrusion and pumping.

MODEL

Roll

Ship's roll is a function of the design characteristics of the vessel, sea state and to a lesser extent the wave period. The roll period of the ship is a characteristic response to most surface waves and the half angle of the roll is an indicator of sea state. Ship's roll motion may be translated into vertical motion of the net by knowing the relationship of the end of the winch boom to the ship's center of gravity. These terms are related in the figure below:



where R = radial distance from center of gravity (C/G) to the end of the winch boom,

V = vertical distance from C/G to end of boom at its resting position,

θ = angle from the horizontal, C/G to end of boom,

X = variable = vertical position of the end of the boom where up is positive and down is negative.

The motion of the ship may be described by letting

A = half angle of ship's roll,

P = period of ship's roll,

t = variable = time.

A time dependent description of the ship's angular motion (y) is thus:

$$y = A\ \mathrm{Sin}\left(\frac{2\pi t}{P}\right).$$

So that the vertical position of the end of the boom (X) relative to C/G is:

$$X = R\ \mathrm{Sin}\ (\theta + y)$$

$$X = R\ \mathrm{Sin}\ \left(\mathrm{Arcsin}\ (V/R) + A\ \mathrm{Sin}\left(\frac{2\pi t}{P}\right)\right).$$

and the velocity of the end of the boom is:

$$\frac{dX}{dt} = R(A)\left(\frac{2\pi}{P}\right)\mathrm{Cos}\left(\frac{2\pi t}{P}\right)\mathrm{Cos}\ \left(\mathrm{Arcsin}\ (V/R) + A\ \mathrm{Sin}\left(\frac{2\pi t}{P}\right)\right).$$

Heave

Heave of the ship is defined as the vertical motion experienced by a vessel as a wave passes under the hull. Ocean swell may be represented simply as a Sin wave:

$$X_w = \frac{H}{2}\ \mathrm{Sin}\left(\frac{2\pi t}{P_w}\right)$$

where

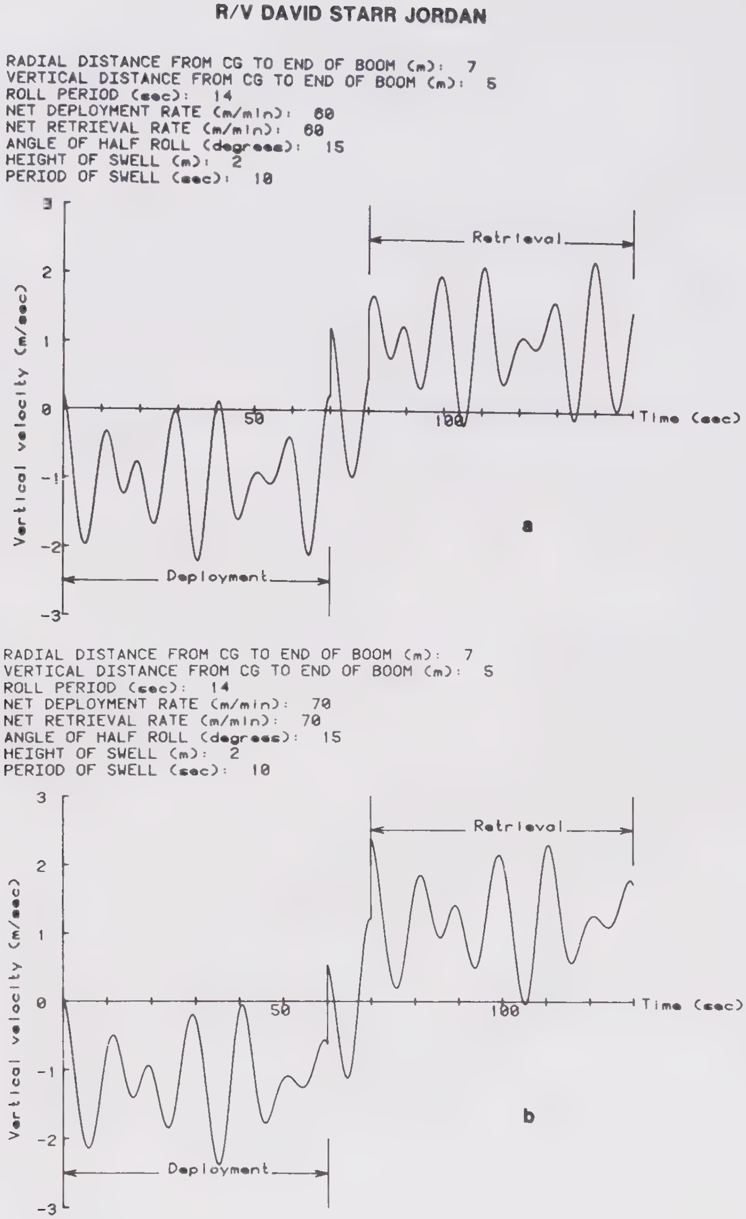
X_w = vertical displacement (heave) of the ship,

H = height of the swell (trough to peak),

P_w = period of the swell (peak to peak).

Vertical velocity due to heave is:

$$\frac{dX_w}{dt} = \frac{H\pi}{P_w}\ \mathrm{Cos}\left(\frac{2\pi t}{P_w}\right)$$



R/V DAVID STARR JORDAN

RADIAL DISTANCE FROM CG TO END OF BOOM (m): 7
VERTICAL DISTANCE FROM CG TO END OF BOOM (m): 5
ROLL PERIOD (sec): 14
NET DEPLOYMENT RATE (m/min): 60
NET RETRIEVAL RATE (m/min): 60
ANGLE OF HALF ROLL (degrees): 15
HEIGHT OF SWELL (m): 2
PERIOD OF SWELL (sec): 10

RADIAL DISTANCE FROM CG TO END OF BOOM (m): 7
VERTICAL DISTANCE FROM CG TO END OF BOOM (m): 5
ROLL PERIOD (sec): 14
NET DEPLOYMENT RATE (m/min): 70
NET RETRIEVAL RATE (m/min): 70
ANGLE OF HALF ROLL (degrees): 15
HEIGHT OF SWELL (m): 2
PERIOD OF SWELL (sec): 10

FIG. 2. The effect of net retrieval rate on the vertical velocity of the net. Simulations were conducted fore the R/V *David Starr Jordan* and a "worst case" sea state.

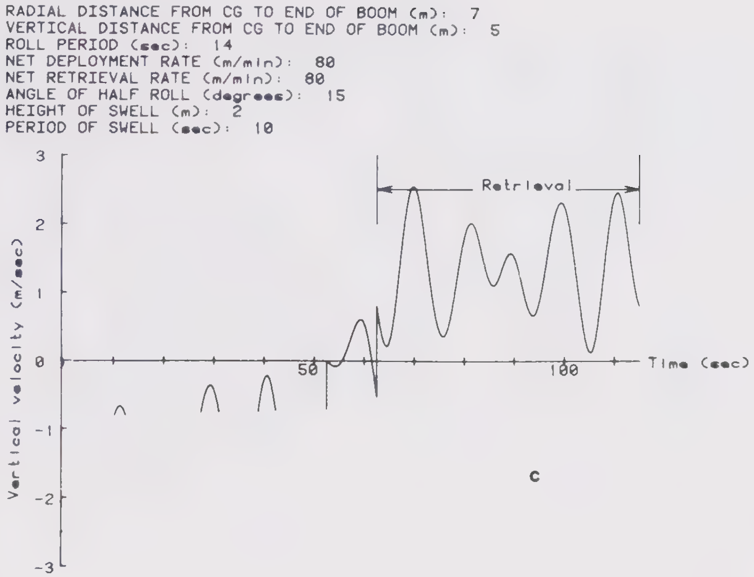

RADIAL DISTANCE FROM CG TO END OF BOOM (m): 7
VERTICAL DISTANCE FROM CG TO END OF BOOM (m): 5
ROLL PERIOD (sec): 14
NET DEPLOYMENT RATE (m/min): 80
NET RETRIEVAL RATE (m/min): 80
ANGLE OF HALF ROLL (degrees): 15
HEIGHT OF SWELL (m): 2
PERIOD OF SWELL (sec): 10

FIG. 2 (continued)

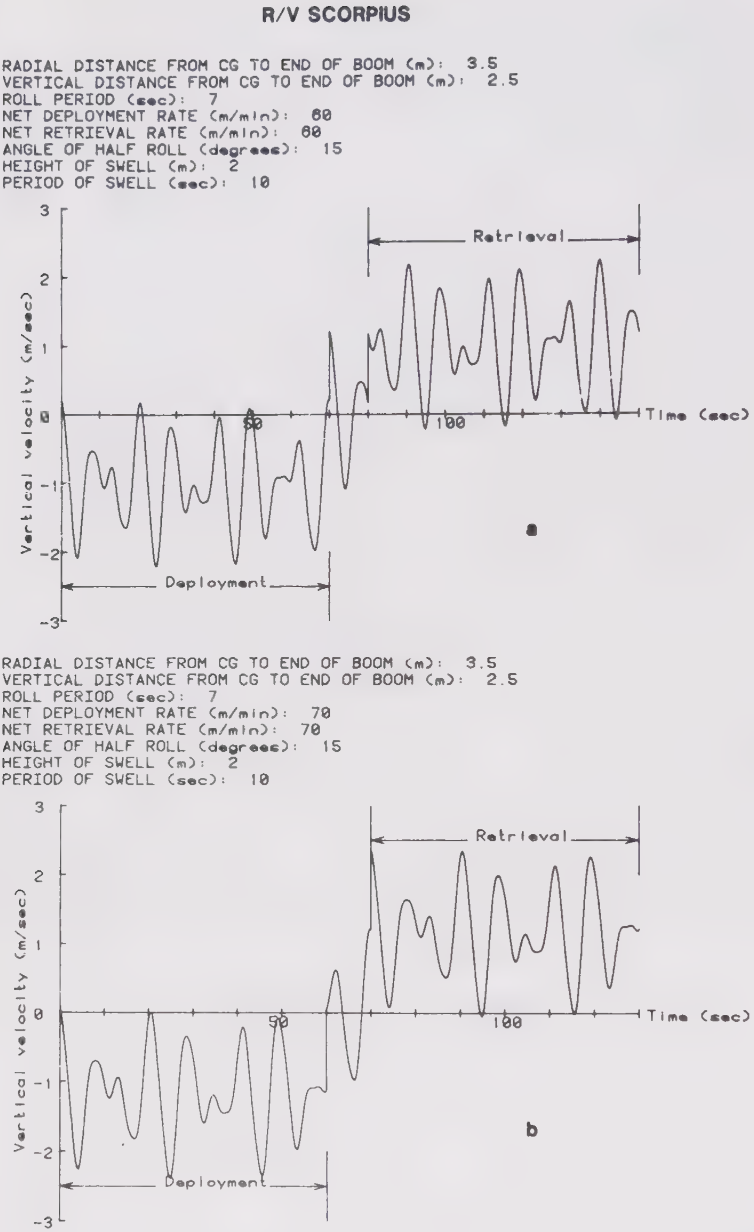
Movement of the Net

The vertical velocity of the net (S) is estimated as the sum of the vertical motions of roll, heave and net retrieval (N):

$$S = N + \frac{dx}{dt} + \frac{dx_w}{dt}$$

EXAMPLE

Velocity of the net during retrieval is the critical variable: it should always be greater than zero to prevent loss of sample by pumping and should not exceed 2 m/sec to prevent loss of sample by extrusion. The ship's design



R/V SCORPIUS

RADIAL DISTANCE FROM CG TO END OF BOOM (m): 3.5
VERTICAL DISTANCE FROM CG TO END OF BOOM (m): 2.5
ROLL PERIOD (sec): 7
NET DEPLOYMENT RATE (m/min): 60
NET RETRIEVAL RATE (m/min): 60
ANGLE OF HALF ROLL (degrees): 15
HEIGHT OF SWELL (m): 2
PERIOD OF SWELL (sec): 10

RADIAL DISTANCE FROM CG TO END OF BOOM (m): 3.5
VERTICAL DISTANCE FROM CG TO END OF BOOM (m): 2.5
ROLL PERIOD (sec): 7
NET DEPLOYMENT RATE (m/min): 70
NET RETRIEVAL RATE (m/min): 70
ANGLE OF HALF ROLL (degrees): 15
HEIGHT OF SWELL (m): 2
PERIOD OF SWELL (sec): 10

FIG. 3. The effect of net retrieval rate on the vertical velocity of the net. Simulations were conducted for the R/V *Scorpius* and a "worst case" sea state.

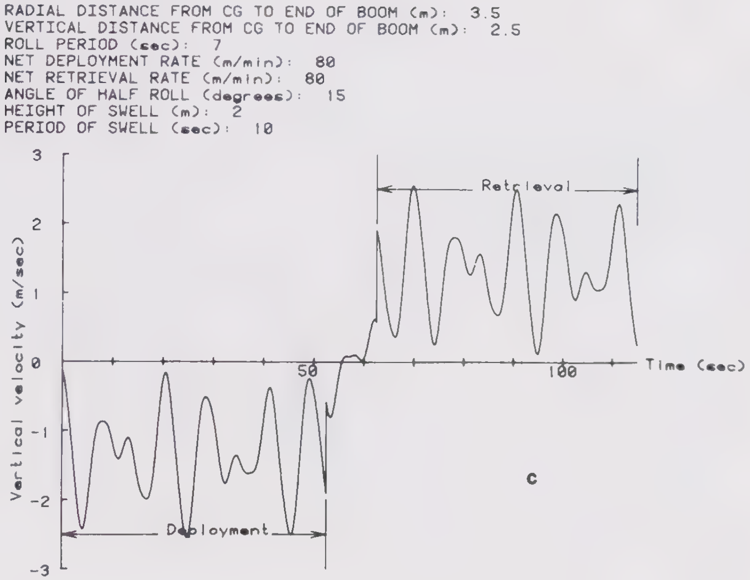
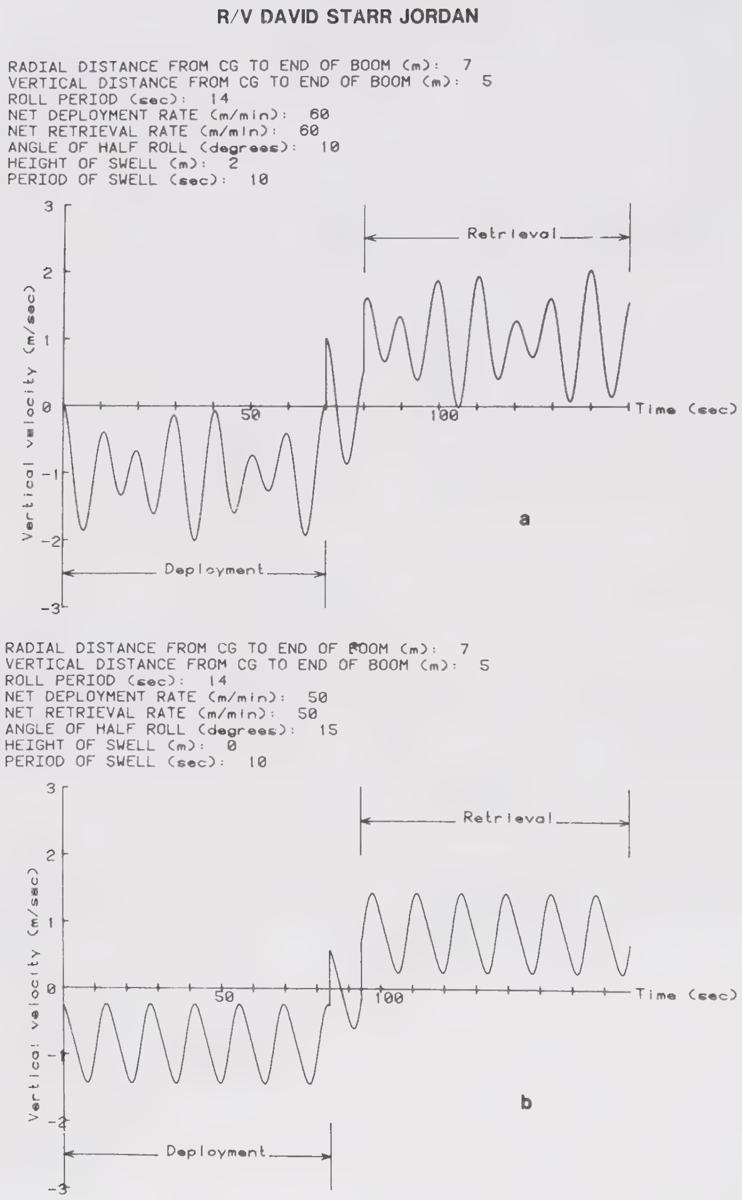


FIG. 3 (continued)

characteristics and sea state are specified and the time course of net velocity can be plotted; the existence and extent of critical velocities may be determined from visual inspection of the plots.

I assumed ship design characteristics similar to the R/V David Starr Jordan and also to a vessel one-half her size, similar to the R/V Scorpius. I assumed the ship's half-roll angle to be 15°; i.e., CalVET sampling would be suspended during sea states which caused ship's roll to exceed 15° from the vertical. I further imposed a 2 m swell with a 10 sec period. The circumstances are thus "worst case" and the simulations were made at different retrieval rates in a search for the minimal rate which will prevent pumping (Figures 2 and 3). The simulation may also be run (Figure 4),at different sea states and ship designs, as a sensitivity study. Criteria may be specified for suspension of operations due to weather for specific vessels.



R/V DAVID STARR JORDAN

RADIAL DISTANCE FROM CG TO END OF BOOM (m): 7
VERTICAL DISTANCE FROM CG TO END OF BOOM (m): 5
ROLL PERIOD (sec): 14
NET DEPLOYMENT RATE (m/min): 60
NET RETRIEVAL RATE (m/min): 60
ANGLE OF HALF ROLL (degrees): 10
HEIGHT OF SWELL (m): 2
PERIOD OF SWELL (sec): 10

RADIAL DISTANCE FROM CG TO END OF BOOM (m): 7
VERTICAL DISTANCE FROM CG TO END OF BOOM (m): 5
ROLL PERIOD (sec): 14
NET DEPLOYMENT RATE (m/min): 50
NET RETRIEVAL RATE (m/min): 50
ANGLE OF HALF ROLL (degrees): 15
HEIGHT OF SWELL (m): 0
PERIOD OF SWELL (sec): 10

FIG. 4. The effect of sea state on the minimum net retrieval rate. Simulations were conducted for the R/V David Starr Jordan.

RECOMMENDATION

If field operations continue under conditions in which the ship's half-roll angle does not exceed 15° and if the ground swell does not exceed 2 m (trough to peak), then the optimal net retrieval rate is 70 m/sec on both the R/V *David Starr Jordan* (Figure 2) and the R/V *Scorpius* (Figure 3). At 60 m/sec "pumping" is evident (Figures 2a and 3a); at 80 m/sec the velocity of the net exceeds 2 m/sec for a considerable amount of time (Figures 2c and 3c).

The ship's heave due to ground swell generates more sampling problems than the ship's roll. The R/V *Jordan* could retrieve the net at 60 m/sec if operations were suspended when the ship's half-roll angle exceeded 10° (Figure 4a). However the retrieval rate could be lowered to 50 m/sec if there were negligible motion due to heave (Figure 4b).

NEARSHORE PRODUCTION OF YOUNG ANCHOVY

ROGER P. HEWITT
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038

GARY. D. BREWER
University of Southern California
Institute for Marine and Coastal Studies
Los Angeles, California 90007

ABSTRACT

The daily production of northern anchovy eggs and larvae is determined for the nearshore region (within ca. 3 mi of the coast) of the Southern California Bight. Stage-specific catches were obtained from monthly Ichthyoplankton Coastal and Harbor Studies (ICHS) cruises during 1979-80. Age-specific production estimates are derived by pooling and adjusting the catches for growth and sampler bias. Hazard functions are introduced, and a production curve is fit to the data. Production of young anchovy was compared with that for the greater Southern California Bight; there was no evidence for greater production inshore. The spawning cycle and survival of young in the nearshore region reflected that occurring throughout the Southern California Bight.

RESUMEN

Se determina la producción diaria de huevos y larvas de anchoa (*Engraulis mordax*) en la zona costera (a menos de tres millas de la costa) en la región del seno de la California Meridional. Los datos utilizados se basan en la serie de fases de desarrollo, que aparecían en las colecciones del programa de Ictioplancton costero y estudios de estuarios y bahías (ICHS), cruceros 1979-80.

Las estimaciones de edades en esta producción se han determinado agrupando las capturas y ajustándolas en relación al crecimiento y a las variaciones ocasionadas por el muestreo. Funciones del azar se incluyen en los cálculos, ajustando así los datos en la curva resultante. Esta producción de anchoa se compara con la obtenida para todo el seno de la California Meridional, y no hay evidencia de que las aguas costeras presenten una mayor producción. El ciclo de puesta y la supervivencia de los jóvenes en la región costera, reflejan lo que acontece en todo el seno de la California Meridional.

INTRODUCTION

The abundance and distribution of several fish populations off the Pacific coast of North America have been monitored using ichthyopolankton surveys conducted by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) since 1949. These surveys extended from Baja California to Washington state and several hundred km offshore, and were directed at the detection of gross changes in abundance and distribution patterns (Smith 1972). These data have also been used to estimate production and survival of early life stages, with the ultimate goal of explaining and predicting variations in population growth (Smith 1973; Lasker and Smith 1977; Zweifel and Smith 1981; Hewitt 1981; Hewitt and Methot 1982; Hewitt 1982). The principal species of interest has been the northern anchovy (*Engraulis mordax*), partly because of its importance in the natural economy of the California Current and partly because it is typical of clupeoid populations, which are highly productive and support some of the largest fisheries in the world.

Another source of ichthyoplankton data is the Ichthyoplankton Coastal and Harbor Studies (ICHS) (Brewer et al. 1980; Brewer and Smith 1982). During this project the nearshore zone of the Southern California Bight was sampled monthly from June 1978 through July 1980. This zone, within ca. 3 miles of the coast, often harbors high densities of phytoplankton and microzooplankton (Eppley et al. 1978; Beers and Stewart 1967; Lasker 1981) and may also be a region of enhanced larval survival and elevated anchovy productivity.

Brewer and Smith (1982) described the ICHS collections of anchovy and sardine (*Sardinops caerulea*) eggs and larvae. They reported that the seasonal cycle and standing stock of anchovy eggs and larvae in the nearshore zone were comparable to those estimated for the greater Southern California Bight from CalCOFI surveys. The nearshore region accounted for 3.8% of the area and 3% of the larvae contained by the greater Southern California Bight. Brewer and Smith concluded that the nearshore zone was not a preferred spawning habitat; however, they withheld judgment on the importance of the region as a nursery ground.

In this paper we compare the production of larval anchovy in the nearshore zone with that throughout the Southern California Bight. We pooled stage-specific catches through the 1980 spawning season

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[Manuscript received February 4, 1983.]

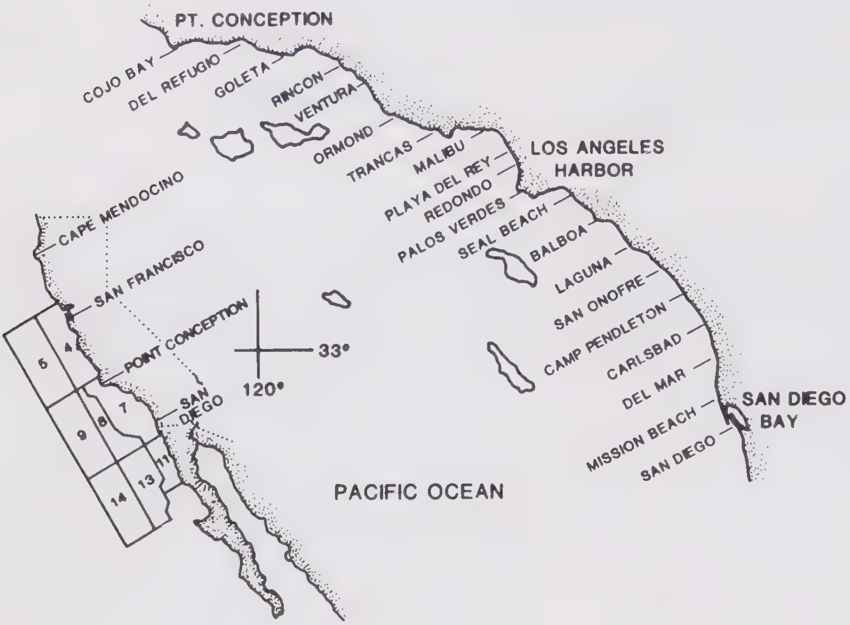

Figure 1. The Ichthyoplankton Coastal and Harbor Studies (ICHS) sampled 20 transects in the nearshore zone (within 3 miles of the coast) of the Southern California Bight between Point Conception and San Diego. Region 7 of the CalCOFI sampling grid is defined here as the greater Southern California Bight (inset).

and derived age-specific production estimates by adjusting the catches for growth and sampler bias. We briefly discuss three hazard functions and fit production curves to the data. Finally, we contrast the curves from the two regions and discuss their interpretation.

MATERIALS AND METHODS

We define the greater Southern California Bight as CalCOFI region 7, encompassing the area between Point Conception and the international border at San Diego, and seaward approximately 200 km (Figure 1). The nearshore zone is defined as that portion of the bight within the 43-m isobath and the mainland coast, and contains 2,652 km^2 (3.8%) of the total 69,055 km^2 area of CalCOFI region 7. The data reported here were obtained from August 1979 through July 1980 (ICHS Phase II; Brewer and Smith 1982), and the production comparisons were made for the 1980 spawning season (January through June 1980).

The ICHS sampling regime consisted of 46 stations, along 20 transects, that were occupied each month. Stations were positioned over the 8-m and 22-m isobaths on each transect and additionally over the 15-m and 36-m isobaths on the Ormond, Redondo, and San Onofre transects (Figure 1). The sampling gear was a 70-cm diameter bongo frame, fitted with 333-micrometer mesh Nitex nets and an opening-closing device. The gear was deployed to the bottom; the net apertures were opened; and the gear was retrieved obliquely to the surface, filtering an average of 8.1 m^3 of water per m of depth fished. Additional details regarding sampling techniques and laboratory procedures are described by Brewer and Smith (1982).

CalCOFI region 7 was sampled during four cruises conducted in March, April, and May 1980. Two gear types and respective station grids were employed. The first was a 70-cm oblique bongo tow deployed on standard CalCOFI stations; the net was 505-micrometer Nitex with no opening-closing device, fished to 210-m depth and filtering an average of 3.7 m^3 per m of depth (see Stauffer and Picquelle 1981, for a description of these cruises, and Kramer et al. 1972, Smith and Richardson 1977, for sampling techniques and laboratory procedures). The second gear was a 25-cm diameter frame, with a 333-micron Nitex net, deployed to 70-m depth and retrieved vertically (see Hewitt, in press, for a brief description of the CalCOFI vertical egg tow-CalVET sampler). The CalVET sampler was deployed over a dense grid of stations with the purpose of intensively sampling anchovy egg production.[1]

Plankton samples were preserved and returned to the laboratory, where they were sorted, and the anchovy eggs and larvae were identified and enumer-

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[1] Stauffer, G. D., and S. J. Picquelle. MS. Egg production estimates of spawning biomass of the northern anchovy for 1980 and 1981.

TABLE 1

Survey Cruises Contributing to the ICHS Sample of the Nearshore Zone and the CalCOFI Sample of the Greater Southern California Bight (Region 7)*

Cruise designation	Dates	Number of stations	Percent positive	Egg density (#/m²)	Larval density (#/m²)
ICHS	1979				
15	13-24 Aug	46	98	38	20
16	10-21 Sept	46	100	3	15
17	8-18 Oct	46	85	22	4
18	5-16 Nov	46	54	15	3
19	3-13 Dec	46	78	69	9
	1980				
20	7-19 Jan	46	91	70	81
21	11-28 Feb	46	100	191	91
22	10-22 Mar	46	98	295	195
23	7-17 Apr	46	100	124	50
24	12-25 May	46	93	34	22
25	16-26 June	46	87	6	7
26	14-25 July	46	65	4	2
CalCOFI bongo					
8003TK	24 Feb-2 Mar	24	100	——	106
8003JD	27 Mar-6 Apr	20	95	——	204
8005JD	11 Apr-29 Apr	29	90	——	94
8005JD	24 May-30 May	24	71	——	57
CalCOFI CalVET					
8003/04JD	27 Mar-29 Apr	458	64	326	——

*The sample obtained with the CalVET net includes tows made in regions 8 and 11 as well.

ated by developmental stage. Results were expressed in numbers of eggs or larvae under 1 m² of sea-surface area.

RESULTS

Standing Stock

Anchovy eggs and larvae were caught at most stations during every ICHS survey (Table 1). On the other hand, the density of eggs and larvae varied two orders of magnitude as the spawning season progressed. Low spawning activity in the fall is followed by an increase in spawning in December, achieving a maximum in March and declining through July. The bell-shaped seasonal spawning curve (Figure 2) is similar to that found throughout the spawning habitat (Brewer and Smith 1982; Hewitt 1980; Hewitt and Methot 1982).

Seasonal catches by stage are described in Figure 3. Nine percent of the year's catch was taken between August and November. The early fall spawning peak, apparent in the August survey, was limited to the western portion of the Santa Barbara Channel. Very little spawning occurred in September and October, and larger larvae (10-mm mode in September, 15-mm mode in October) were encountered in Santa Monica Bay. Some spawning and small larvae were detected in the Santa Barbara Channel in November. By December, spawning increased in intensity and spread south and east to Santa Monica Bay. In January spawning extended from the Santa Barbara Channel to the Los Angeles harbor, and larger larvae were evident from the December spawning. By February, spawning was evident from the Santa Barbara Channel to San Diego and peaked in March with extensive spawning all along the coast. In April, May, and June spawning was progressively reduced and displaced southward. By July very little reproduction was evident; catches of large larvae from the previous months' spawning were made along the coast between Los Angeles and San Diego.

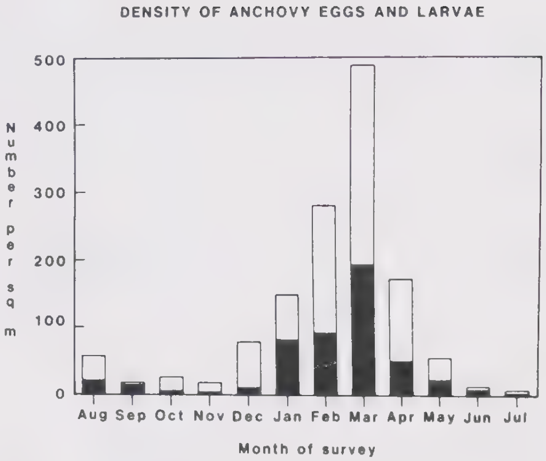

Figure 2. Densities (number under 1 m² of sea-surface area) of anchovy eggs (clear) and larvae (shaded) in the nearshore zone by survey month. The bell-shaped spawning curve is similar to that observed throughout the spawning habitat.

Data from the January through June cruises were pooled to draw the composite catch curve (Figure 4). These data constitute 85% of all the eggs and larvae retained, and describe the rise, peak, and decline of the spawning cycle.

Production

To appreciate trophic dynamics, and more specifically to assess the biological importance of a region, one must consider the flux of organic material (or production) rather than the simple standing stock. To do so we assumed that the average standing stock by stage was representative of a single cohort as it progressed through the larval period. This is the critical assumption and implies steady-state production of eggs and a stable age distribution. That eggs are continually produced in the population is supported by estimates that the average female spawns every 7 to 10 days during the spawning season (Hunter and Gold-

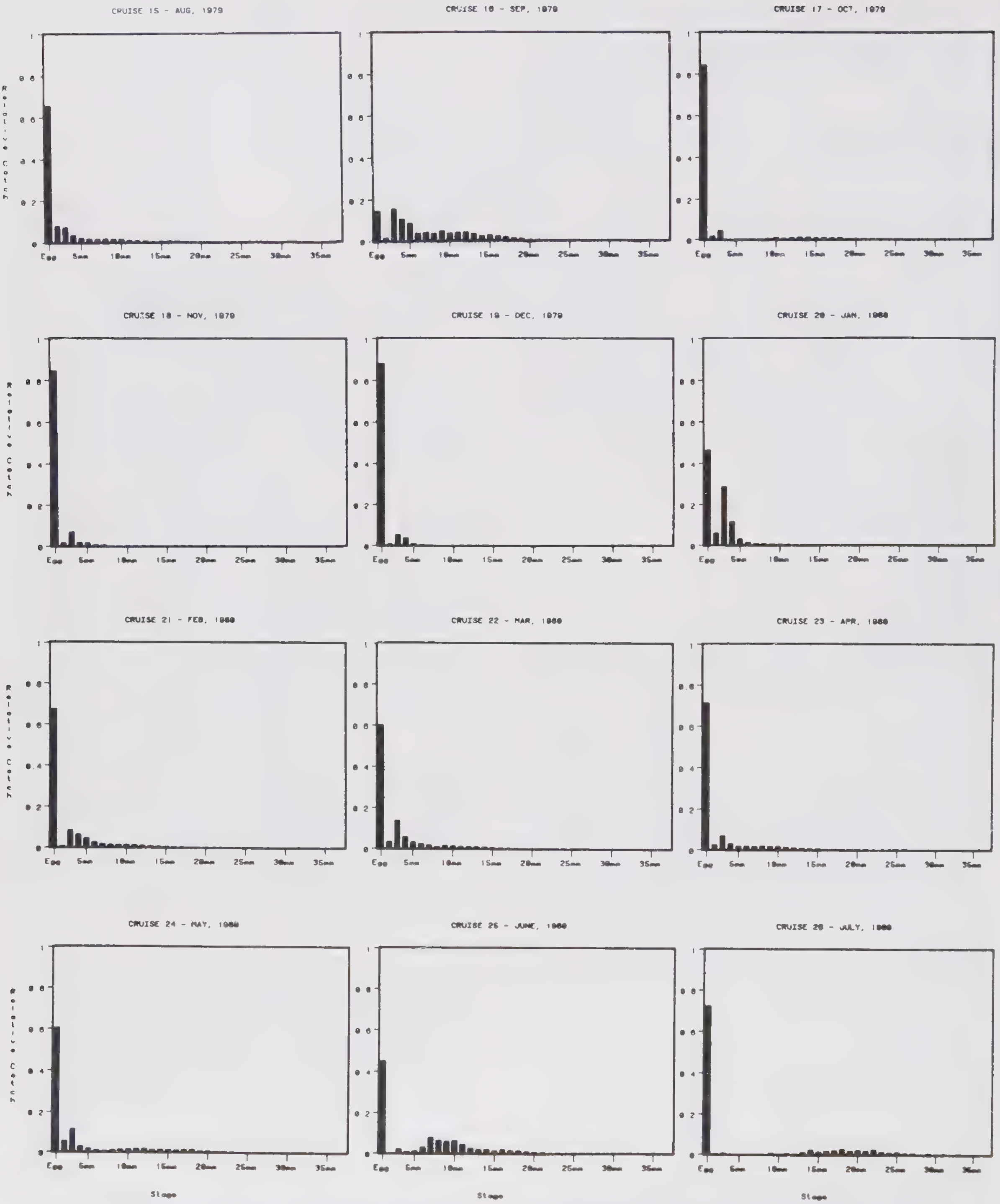

Figure 3. Relative catches by stage for each ICHS survey month reflect the seasonal spawning curve. Egg production in August resulted in catches of large larvae in September and October; large larvae again became a substantial portion of the catch in May, June, and July when egg production rapidly declined.

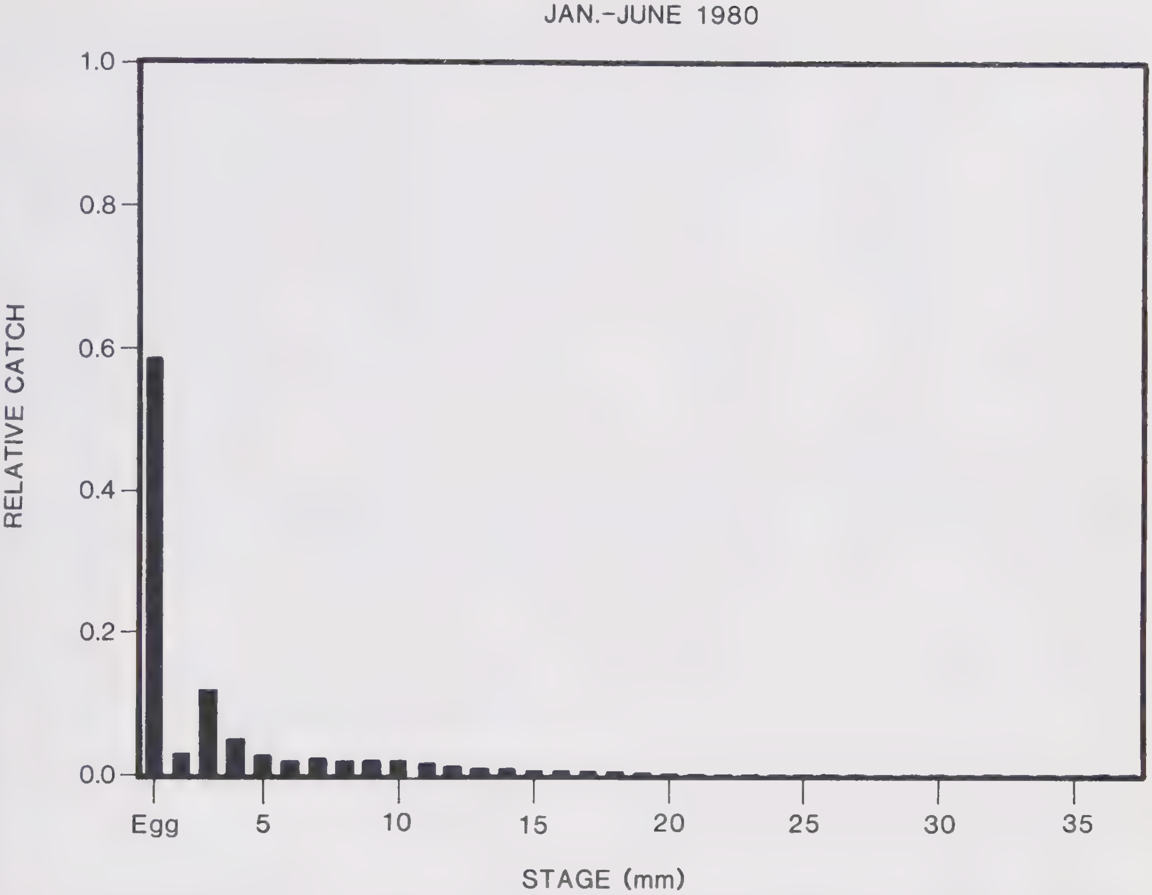

Figure 4. · The average catch curve for the ICHS surveys conducted during the period January through June accounts for 85% of all eggs and larvae retained. These data were collected through the rise, peak, and decline of the spawning season. We assumed that the average standing stock by stage was representative of a single cohort as it passed through the larval period

berg 1980; Hunter and Macewicz 1980; Picquelle and Hewitt 1983). Hewitt and Methot (1982) showed that an unbiased age distribution may be obtained by pooling data collected through the spawning season.[2]

The pooled catch curve (Figure 4) was then adjusted for sampling bias and variability: individual observations were adjusted for variations in the volume of water filtered per m of depth; bias corrections were applied for extrusion of small larvae through the meshes of the net; and the adjusted catches were divided by the duration of growth, through each stage, to estimate the age-specific production rate (P_t). The adjustments were accomplished by fitting a weighted negative binomial model to the sample frequency distributions of each size class. Each observation was weighted by a factor that is the product of the various adjustments, and the means of the final distributions are unbiased estimates of production (P_t). The procedure was developed in a series of papers: Bissel 1972; Zweifel and Smith 1981; Hewitt 1981, 1982; Hewitt and Methot 1982. The calculations are summarized in Table 2, and the results are described in Figure 5.

Estimates of production declined with age as the larvae starved or were preyed upon (Figure 5); initial mortality was severe and abated somewhat as the larvae developed. Our intention was to describe these data with a functional form; this curve is sometimes referred to as the mortality curve or, conversely, the survival curve; here we label it the production curve.

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[2] Alternately one may plot the seasonal curves of daily production for each stage and estimate total seasonal production as the area under the curves (Bannister et al. 1974). This method and the one described in the text yield essentially the same results, i.e., total seasonal production estimated from the seasonal curves of daily production is not different from the average daily production summed over the averaging period. Furthermore, the rate of decline in production with age is also the same.

TABLE 2
Size-Specific Catches of Anchovy Larvae and Age-Specific Estimates of Daily Production

Preserved size (mm)	Fraction retained in net[1]	Average adjustment for sampling and sorting variability[2]	Average duration of growth[3]	Average catch $\left(\frac{\text{number}}{\text{tow}}\right)$	P_t $\left(\frac{\text{number}}{\text{m}^2\text{-day}}\right)$[4]	Age since fertilization (days)
Egg	0.917	15.848	2.43	1978.61	56.03	1.22
1.75	0.630	1.087	0.38	5.98	22.99	2.63
2.75	0.630	0.998	2.93	25.12	13.64	4.28
3.75	0.630	1.214	3.34	12.36	4.84	7.44
4.75	0.950	1.244	2.48	6.36	2.17	10.34
5.75	1.000	1.457	2.28	4.55	1.37	12.74
6.75	1.000	1.699	2.13	4.09	1.13	14.76
7.75	1.000	1.957	2.05	3.65	0.91	16.91
8.75	1.000	1.862	2.01	3.93	1.05	18.85
9.75	1.000	1.954	1.99	3.85	0.99	20.88
10.75	1.000	2.084	1.99	3.11	0.75	22.78
11.75	1.000	2.040	2.00	2.53	0.62	24.80
12.75	1.000	2.199	2.06	2.31	0.51	26.73
13.75	1.000	2.246	2.12	2.00	0.42	28.80

1. Extrusion corrections are based on relative retention rates between 75-micrometer and 333-micrometer mesh nets (Lo, in press).
2. Accounts for partial sorting of samples, and standardizes sampling volume to 1m^3 per m of depth. An average of 17% of the larvae were sized.
3. Temperature-dependent embryonic growth is determined from laboratory experiment (Lo, in press), and post-yolk-sac growth follows Methot's (1981) description.
4. Production rates (P_t) may be estimated by dividing the average catch by the product of columns 2, 3, and 4. In practice however, P_t is the mean of a weighted negative binomial model fit to the distribution of individual observations (i.e., plankton tows).

To begin, we model the mortality as a portion of those living:

$$\frac{dp}{dt} = P\,Z(t)$$

where P is the production rate, t is age, and $Z(t)$ is the hazard function (Watson and Leadbetter 1964), also referred to as the conditional failure rate, age-specific death rate, or instantaneous mortality rate. By integrating the expression from O to t we can express the probability of an animal's living to time t as:

$$\frac{P_t}{P_o} = \exp\left(\int_o^t z(t)dt\right) \quad .$$

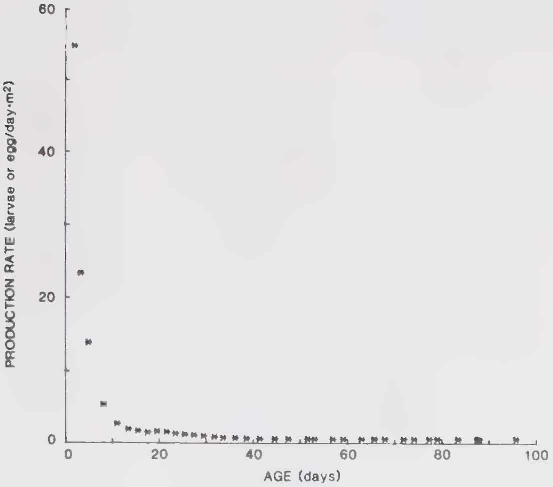

Figure 5. Estimates of age-specific production rates were derived from the pooled catch curve by adjusting the catches for growth and sampler bias. A production curve fit to these data must describe initially severe mortality, which abates somewhat as the larvae develop.

By rearrangement the production curve is:

$$P_t = P_o \exp\left(\int_o^t z(t)dt\right) \quad .$$

Several forms may be used for $Z(t)$; here we describe the consequences of three. Because animals are dying, the hazard function is always negative.

$$\text{Case 1: } Z(t) = -Z \text{ (a constant)}$$

This is the well-known constant mortality or exponential decay model. The production curve becomes:

$$P_t = P_o\, e^{-Zt} \quad .$$

If the population followed this model, the logarithm of the production rate would be a linear function of age, and the slope would be equal to $-Z$. With no increase in the number of parameters, the hazard function can be modeled to decrease with age[3]:

$$\text{Case 2:} \qquad Z(t) = \frac{-\beta}{t} \quad .$$

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[3] Lo, N. MS. Egg production of central stock of northern anchovy: 1951-82

As t increases, $Z(t)$ decreases, describing improving survival with age. The production curve becomes:

$$P_t = P_h \left(\frac{t_h}{t}\right)^{\beta} \quad \text{for } t \geqslant t_h$$

Although this form is attractive because only two parameters are required (P_h and β), it cannot be extrapolated to time zero. Picquelle and Hewitt (1983) applied this model to larval production data where t_h is the age of hatching, and time zero is the moment of fertilization. If the population followed this model, the logarithm of the production rate would be a linear function of the logarithm of age. The production curve may be extended to the origin by adding a third parameter (α):

$$\text{Case 3:} \qquad Z(t) = \frac{-\beta}{\alpha + t}$$

This form also describes improving survival with age; in addition, as t approaches zero, $Z(t)$ remains finite. The production curve becomes:

$$P_t = P_o \left(\frac{\alpha}{\alpha + t}\right)^{\beta}$$

As with Case 2, a linear plot of the logarithm of the production rate on the logarithm of age would be consistent with this model.

A semilog plot of production on age (Figure 6A) is nonlinear, particularly at ages less than 20 days, suggesting that a constant mortality model (Case 1) would not be appropriate. During this period aggregated eggs are disbursing and hatching; yolk-sac larvae are developing locomotor abilities; and post-yolk-sac larvae are rapidly acquiring sensory capabilities. Given the rapid ontogeny compressed into this phase of the life history, it may be biologically unreasonable to expect constant mortality. A log-log plot of the data (Figure 6B) is linear with a break at approximately 30 days of age; either of the decreasing mortality models described as Case 2 and Case 3 would be appropriate to describe the first 30 days. We fit the Case 3 model to the age-specific production rates for animals less than 30 days old using a nonlinear least squares method. The resulting production curve is described in Figure 7; parameter values are listed in Table 3. Average egg production over the spawning season (January to June) in the nearshore zone was approximately 190 eggs per day per m^2 (standard error = 25).

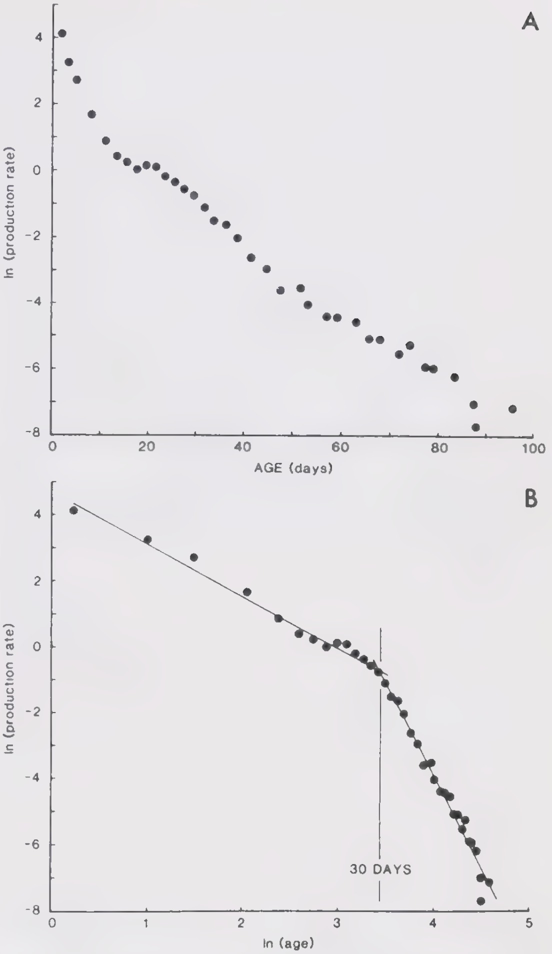

Figure 6 *A.* The semilog plot of production rate on age is nonlinear for the youngest stages, suggesting that the constant mortality model described as Case 1 would be inappropriate.

B. The log-log plot of production rate is linear with an abrupt change in slope at 30 days post fertilization. The lines are drawn by eye for the purpose of emphasizing the linearity and the break point.

TABLE 3

Parameter Values and Production Rate Estimates for Production Curves Fit to the ICHS and CalCOFI Samples

	ICHS		CalCOFI	
Parameter	Parameter value	(Std. error)	Parameter value	(Std. error)
α	1.5	0.42	16.4	9.01
β	2.0	0.22	6.3	2.85
P_o	187.6	24.6	230.2	11.3
$\hat{P}_{10}$	3.0	—	11.4	—
$\hat{P}_{20}$	0.8	—	1.5	—
$\hat{P}_{30}$	0.4	—	0.4	—

Data representing the greater Southern California Bight are drawn from two sources: CalVET and bongo samples (Figure 8). The CalVET sample is a collection of observations made with a small vertical tow designed to sample pelagic fish eggs. These

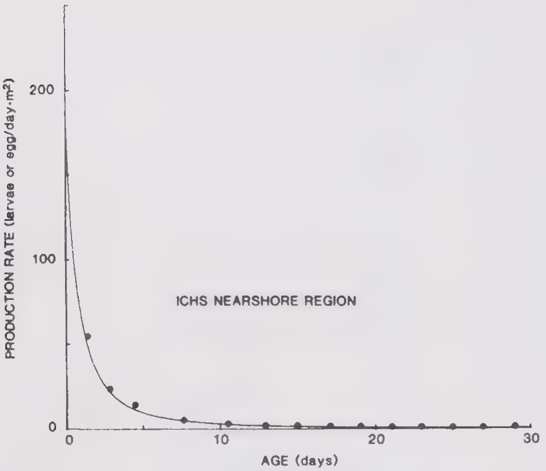

Figure 7. The production curve for the ICHS nearshore zone is of the form described as Case 3, and is fit to the production rate estimates for larvae less than 30 days old.

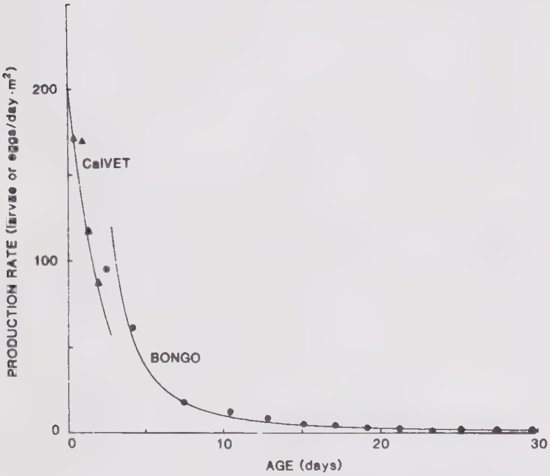

Figure 8. Anchovy egg and larvae production rates for the greater Southern California Bight are estimated from CalVET and bongo net samples obtained in CalCOFI region 7 during March, April, and May. The production curve fit to the CalVET data is of the form described as Case 1; the production curve fit to the bongo data is of the form described as Case 2.

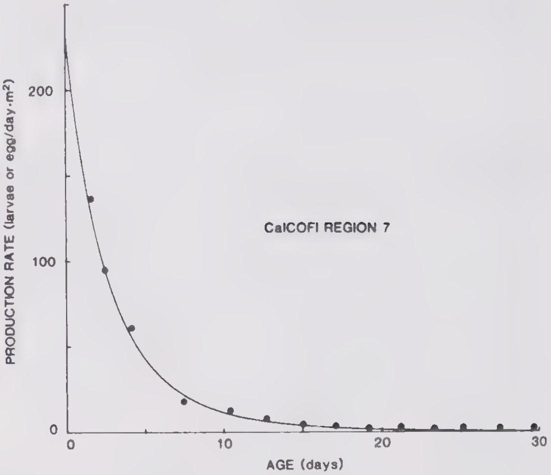

Figure 9. The production curve for the greater Southern California Bight (CalCOFI region 7) is of the form described as Case 3, and is fit to production rate estimates derived from both the CalVET and bongo samples.

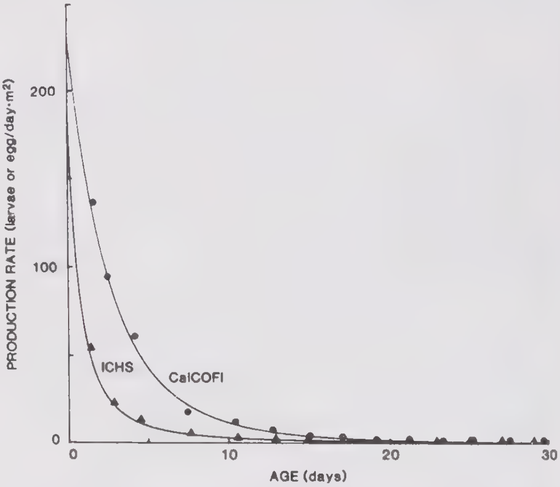

Figure 10. Initial egg production rates in the nearshore zone (ICHS sample) and the greater Southern California Bight (CalCOFI sample) are comparable. Mortality on eggs and yolk-sac larvae appears to be more severe in the nearshore zone; however, the production of 30-day-old larvae is again comparable between the two regions.

data are presented as estimates of egg production in half-day increments over the incubation period (2.8 days at an average temperature of 15.15°C). Stauffer and Picquelle[4] fit the egg-production curve using the constant mortality model described as Case 1. The bongo sample is a collection of observations made with a larger, oblique tow designed to sample larvae. The production curve is the functional form described as Case 2 proposed by Lo[5] and is analogous to analyses reported by Picquelle and Hewitt (1983). Although the sampling gears are quite different in design, they generate complementary and consistent data (Figure 8). The data were merged, and a single production curve (Case 3 functional form) was fit (Figure 9 and Table 3). Although a constant mortality for eggs and variable mortality for larvae may be biologically reasonable, a two-phase production curve is indistinguishable from the single curve for this data set. Average egg production over March, April, and May in the greater Southern California Bight was approximately 230 eggs per day per m^2 (standard error = 11).

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[4] See footnote 1 on page 236

[5] See footnote 3 on page 240

The production curves for the nearshore zone (ICHS) and for the greater Southern California Bight (CalCOFI region 7) are superimposed in Figure 10. Initial production of eggs is comparable in both areas, although early mortality appears to be more severe in the nearshore zone. Later mortality in the nearshore zone is less severe, and the production of 30-day-old larvae is comparable between the two areas.

DISCUSSION

The primary conclusion that may be drawn from these data is that there is no evidence for enhanced production of young anchovy larvae in the nearshore zone. In addition, differences between the shapes of the production curves (Figure 10) are provocative. Anchovy eggs and yolk-sac larvae appear to suffer a more severe mortality in the nearshore zone than in the Southern California Bight. These are also the stages that are most contagious (patchy) in their distribution patterns (Hewitt 1981, 1982), and the most proximate to the adult schools that spawned them. Cannibalism on anchovy eggs is a significant source of mortality (Hunter and Kimbrell 1980), and it may be that the restricted depth range of the nearshore zone acts to increase the incidence of cannibalism. Higher densities of juvenile anchovy and general planktivores in the nearshore zone may cause heavier predation on these stages, which are very aggregated and not yet fully mobile.

Nearshore survival of feeding larvae appears to improve so that the production of 30-day-old larvae in the nearshore zone is comparable to that in the greater Southern California Bight at 0.4 larvae per day per m^2. The improved survival in the nearshore zone may be due to better feeding conditions, although Methot (1981) reported that most young anchovy were growing at the maximum rate, suggesting that food may not be limiting their survival. Increased turbidity of nearshore water may enhance protection from visually oriented predators, but this advantage must be offset partially by the increased density of predators. Regardless of the cause, if the difference in survival rates continued into the juvenile stage, then the nearshore zone would be an area of enhanced anchovy productivity. This question cannot be addressed until methods are developed to effectively sample late larvae and juvenile fish.

Large larvae were caught during the ICHS cruises, although the downward bend in the production curve at 30 days (Figure 6B) suggests that larvae either entered a region of higher mortality or they were increasingly able to avoid the sampling gear. The CalCOFI data also displayed a change in the slope of the production curve at 30 days, and because of the causal ambiguity we eliminated older larvae from the analyses. After comparing the day and night catches of successively larger larvae, Hewitt and Methot (1982) suggested that anchovy larvae, 30 days and older, are increasingly able to avoid capture at night as well as during the day. The ICHS sample contained a greater fraction of large larvae than the CalCOFI sample, although less than would be expected from an extension of the production curve beyond 30 days. Larger larvae become increasingly aggregated as they adopt the schooling habit (Hewitt 1981), and it may be that the difference between the data sets is because the ICHS gear samples a much larger volume of water per tow and thus increases the probability of encountering an aggregation of large larvae. With this interpretation, the difference in catch rates of large larvae may not represent a density difference so much as an example of a problem with sampler threshold. Alternately, the density of large larvae may indeed be higher in the nearshore zone; again this question cannot be addressed until more appropriate samplers are developed.

The critical assumption involved in deriving a production curve from catch data is that a stable age distribution prevails. The errors introduced by seasonal variation in egg production can be minimized by pooling data collected throughout the spawning season (Hewitt and Methot 1982), as we have done with the ICHS surveys.

Immigration and emigration of eggs and larvae to and from the nearshore zone may also upset the assumption of a stable age distribution. Because we are comparing production between regions, we cannot pool spatially as we did temporally and must therefore examine the monthly distribution maps and catch curves for evidence of larvae moving in or out of the nearshore zone. There was nothing to suggest significant immigration or emigration: larvae were more dispersed but encountered in the same general area as eggs; egg production in August resulted in catches of large larvae in September and October; large larvae again became a substantial portion of the catch in May, June, and July, when egg production rapidly decreased. If there was constant transport into the nearshore zone, the apparent mortality would tend toward that of the bight;

whereas constant transport out of the nearshore zone would tend to exaggerate the apparent mortality relative to that of the bight. In fact, neither transport nor spawning are steady through the season and may interact to produce a complex pattern of effects. However, the continuity of geographic patterns between stages and from survey to survey suggests that these effects are not great.

The survey data presented here suggest that production of young anchovy (less than 30 days old) in the nearshore zone is representative of production throughout the greater Southern California Bight. The seasonal production cycle, the density, and the survival of spawn are comparable between the regions. We emphasize, however, our lack of knowledge regarding the late larval and juvenile stages; until this can be improved, the significance of the nearshore zone to anchovy production cannot be fully appreciated.

ACKNOWLEDGMENTS

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Commentary

On the Determinants of Stock Abundance

John R. Hunter
Southwest Fisheries Center, National Marine Fisheries Service

In this commentary I focus on four issues discussed in Warren Wooster's report (Determinants of Stock Abundance) which I feel warrant additional discussion or amplification. In no manner should this commentary be considered an appraisal or review of Wooster's report on Fish Ecology III (Rothschild and Rooth, 1982). I use quotations from Wooster's report to identify each of the subject areas.

"The planktonic stages of the life history are most affected by environmental conditions"

The planktonic larvae of marine fishes are more directly affected by the environment than other life stages but it may be overlooked that not all larval stages are planktonic. The larval period, after the onset of feeding, is a transitional period between the planktonic embryonic stage (egg and yolk-sac stages) and the nektonic juvenile stage. This transition may occur early in the life history, and the truly planktonic stages may be a short segment of a long larval period. In northern anchovy, this transition occurs over about a 10-day period between the 20th and 30th day (10-15 mm, 16°C) of a 70-day larval period. The following events occur during transition: the larva breaks free from the hydrodynamic realm that is transitional between the viscous realm of the yolk-sac larva and the turbulent realm of the nektonic larva (Weihs, 1980); rods appear in the retina and the lens becomes focusable (O'Connell, 1981); the swim bladder becomes functional permitting greater body mass without loss of bouyancy; diel vertical movement to the water surface each night begins (Hunter and Sanchez, 1976); the transition between integumentary and gill respiration begins (O'Connell, 1981); and schooling begins (Hunter and Coyne, 1982).

These behavioral and structural changes have very important ecological and demographic implications. The change in hydrodynamic regime, and the changes in visual, respiratory and other systems set the stage for the onset of schooling and vertical migration. The onset of schooling reverses a trend of continuing dispersion and declining patchiness of larvae to one of increasing contagion (Hewitt, 1981; Hunter and Coyne, 1982). By the end of the planktonic phase mortality rates are much lower than during the highly vulnerable embryonic period. This fact plus the rapid increase in body weight reverses a trend of rapidly declining cohort biomass to one of increasing cohort biomass. The increase in the biomass of the cohort, and increased aggregation due to schooling imply that nektonic larvae occupy the habitat more intensively than planktonic larvae. More intensive occupation of the habitat may increase the likelihood of larval density dependent effects on growth.

Thus the planktonic larval phase is characterized by a pattern of declining contagion (increasing dispersion), high mortality rates, decreasing cohort biomass and a larval existence almost entirely dependent upon the immediate planktonic habitat. In the nektonic larval phase, the larvae become progressively more independent of the immediate planktonic habitat, are capable of extensive vertical movements in search of food, become more aggregated because of schooling, the biomass of the cohort begins to increase and the likelihood of density dependent effects on larval growth increase. Thus interpretation of the effects of the environment on larval survivorship depends upon a thorough knowledge of these developmental changes and the timing of transition from the planktonic to nektonic states. The timing of the transition depends, of course, on the availability of food, as well as temperature specific growth rates.

"The key goal of research on interannual variability of fish stocks is prediction of survivorship until the strength of the year class is identified"

It may never be practical to use the results of larval counts or extensive environmental measurements to provide timely and accurate estimates of year-class strength. In addition, methods already exist for early estimation of year class strength including commercial catches of small fish, trawl or acoustic surveys. I believe the key goal of research on year class variability is to establish how the abundance of the adult stock affects the strength of incoming year classes and to identify the conditions which cause the occasional and remarkable rises or falls in populations (Hunter et al., 1976.) Clearly, the effect of stock size on recruitment is a critical issue since the only option available to managers is regulation of catch.

"It is uncommon to encounter larvae dead of starvation"

I feel partially responsible for this quotation as it reflects perhaps an extreme position that I took in my report for Fish Ecology III. Consequently, I summarize below some of the more important evidence for the relative role played by starvation and predation of marine fish larvae.

Evidence for larval starvation

1. Most laboratory work indicates that marine larvae at the onset of feeding are highly vulnerable to starvation because they search such a small volume of water, have low feeding success, and are unable to withstand prolonged starvation (Hunter, 1981).

2. The food densities required for high survival in the laboratory are not found in the open sea, implying that larvae must depend on the patchiness of food and stable oceanographic conditions to survive (Hunter, 1981).

3. In inshore areas, the incidence of starving anchovy (4-10 mm) using histological criteria (in my mind the only reliable method) was 8% (O'Connell, 1980) and no larvae >10 mm long were starving. In offshore areas about 50% of first feeding jack mackerel larvae were starving but the fraction of starving larvae decreases rapidly with larval age, reaching zero in 2-week-old larvae (G. Theilacker, pers. comm.). These fractions were not adjusted for the duration of the larval stage and cannot be compared to daily mortality rates. On a daily basis the fraction of starving larvae may be lower as the first feeding stage of jack mackerel persists for 2-3 days.

Evidence for predation

1. The highest losses occur during the embryonic period (egg and yolk-sac stages) where starvation can be eliminated as a source of mortality.

2. A great variety of invertebrates and fishes are known to consume eggs and larvae (Hunter, 1981; Bailey and Yen, 1983) and high consumption rates of eggs or larvae have been documented in a few cases (Hunter and Kimbrell, 1981; Möller, 1980).

3. Our most accurate mortality estimates for post-embryonic anchovy (1980-1983) larvae give no sign of an increase in mortality at the onset of feeding. Inaccurate aging might mask the critical period; the first feeding period is the most difficult life stage to assign an age or duration because otoliths cannot be used to age larvae.

4. Growth rates of clupeoid larvae in the sea based on daily increments in otoliths seem to indicate that they grow at the same rates as they do at the laboratory when given abundant food (Blaxter and Hunter, 1982).

5. In large enclosures cod larvae have extremely high survival when predators are excluded and food densities are equivalent to those in the sea (Ellertsen et al., 1981).

These assertions are based on very few field studies and clearly the dominant mechanism may vary among species, habitats and years. What is certain is that the incidence of starvation or slow growth can be documented with greater ease and accuracy than rates of predation because of the existence of starvation-histology and otolith-ageing methodologies. No similar advances have been made that facilitate studies of predation.

> "One must conclude that in recent years meso-scale ichthyoplankton surveys have not greatly improved understanding and Rothschild et al. propose as an alternative, a more holistic approach on trophodynamics of micro- and fine-scale ecosystem"

This point of view reflects an interesting hypothesis which links survival of planktonic larvae to the environment in a novel and functional way (the stability hypothesis, Lasker, 1981). On the other hand, I believe that this is misleading advice for an overall program on recruitment mechanisms when the species spawn over a large geographic area and the localities from which the survivors originate vary unpredictably in space and time. Under these circumstances surveys which delimit the spawning habitat (meso-scale surveys) are essential for the following reasons:

1. Testing of the stability hypothesis or any other larval survival mechanism must be set in the context of the spawning distribution of the population and this information can only be provided by meso-scale surveys. Knowledge of events in a small segment of the population is not sufficient for estimating effects on the population as a whole.

2. Rates of mortality are powerful research tools but they require meso-scale surveys. Mortality rates cannot be measured over a segment of the population because of dispersion and advection of larvae.

3. The annual production of eggs and larvae over the season must be known in order to determine whether changes in year class size are a result of differences in larval mortality or due to differences in the annual or seasonal production of eggs. If the annual egg production is unknown one is unable to use a powerful tool, the birthdate distribution of the juveniles, for assaying the quality of the environment (Methot, 1981).

4. Many of the hypotheses of survivorship of larvae can only be studied on a meso-scale, for example, the larval drift hypothesis and the expansion of spawning range hypothesis of MacCall (1980) and Lasker and MacCall (1983).

5. Most of the significant advances that have been made in recent years on the ecology of northern anchovy were made chiefly as a result of meso-scale surveys.

These comments apply to most of the commercially important marine fish stocks that spawn over a broad geographic area. On the other hand, micro-scale, site intensive studies alone would be preferable under several special circumstances: when the young destined to perpetuate the population originate from a small area that is constant in location and time; or when they originate from an oceanographic feature which is predictable in space and time; or when they suffer the same fate over the entire spawning habitat. Most importantly, the answer to the question of whether or not these special circumstances apply to a given species probably requires spawning-habitat-scale (meso-scale) surveys. Perhaps the failure of many meso-scale surveys has been that they were not sufficiently extensive to delimit the spawning habitat in space and time nor sufficiently intensive to reveal biological processes.

In summary, to limit work on recruitment mechanisms to site intensive microscale studies is not advisable unless documentation exists that the site is truly representative or that it contains most of the potential survivors. If these conditions are not met then use of only site intensive work is to focus on only a few of the possible mortality processes without adequate geographic and temporal context, and to ignore some of the most powerful tools for understanding (birthdate distributions, juvenile abundance, life stage specific mortality rates and variation in spawn distribution). It is certainly important to do such work, not as an alternative to meso-scale research, but in conjunction with it.

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8322

Sea surface temperatures in the northwestern Atlantic in 1980

(Figures 22-34; Tables 4-5)

Sea surface temperature (SST) data, principally collected from cooling water intakes of merchant ships, are reported in radio weather messages and log books transmitted to the U.S. Fleet Numerical Oceanography

Table 4. Monthly average values of air temperature departures (from long-term monthly station means), resultant wind velocity, and scalar wind speed from Atlantic coastal weather stations for November 1980 – January 1981

	Air temperature departure (°C)	Resultant wind direction and speed ($°/m{\cdot}s^{-1}$)	Av. wind speed (m/s)
Portland, Maine			
Nov 80	−1·3	300/2·3	4·2
Dec 80	−2·4	310/2·3	3·7
Jan 81	−4·3	300/2·1	3·4
Boston, Massachusetts			
Nov 80	−2·2	290/3·7	6·2
Dec 80	−2·4	290/3·3	5·0
Jan 81	−4·3	290/4·4	5·8
Providence, Rhode Island			
Nov 80	−1·3	300/2·8	4·7
Dec 80	−1·7	310/2·9	4·4
Jan 81	−4·5	300/2·8	3·8
New York, NY (JFK Intl. Airport)			
Nov 80	−0·6	300/3·9	6·5
Dec 80	−0·7	320/3·9	6·4
Jan 81	−2·7	310/4·1	6·1
Atlantic City, New Jersey			
Nov 80	−2·6	280/2·1	3·8
Dec 80	−2·2	300/2·3	4·1
Jan 81	−5·5	290/2·6	4·0
Norfolk, Virginia			
Nov 80	−0·9	320/1·4	4·8
Dec 80	0·0	350/2·2	5·3
Jan 81	−4·3	330/1·8	4·4

Table 5. Monthly average sea surface temperature anomalies (°C) from the 1948–1967 means for January 1980 – January 1981 in the northwestern Atlantic Ocean (35°–46°N 60°–76°W)

Date	Number of 1°-squares	Area mean anomaly	Standard deviation 1948-1967
Jan	111	+0·20	1·26
Feb	117	−0·31	1·23
Mar	109	−0·28	1·49
Apr	113	+0·12	1·51
May	119	+0·56	1·22
Jun	121	−0·04	0·91
Jul	127	−0·25	0·89
Aug	61	−0·47	0·85
Sep	103	+0·51	0·89
Oct	111	+0·03	0·95
Nov	112	−0·64	0·90
Dec	108	−0·59	0·91
Jan	107	−0·69	1·26

Center (FNOC) and the National Climatic Center for processing and archiving. The "real-time" reports of the data base provided by the radio messages are analyzed by FNOC and the Pacific Environmental Group of the National Marine Fisheries Service, which is co-located with FNOC. An elementary step in the analysis is the computation of average monthly temperatures and anomalies (from 1948-1967 means) for each 1° × 1° square for which enough data have been reported each month. The average SSTs, anomalies, and number of

Figures 22-34. Average sea surface temperature anomalies (°C). Also shown in each one-degree square are average sea surface temperatures (upper number) and the number of observations (lower number).

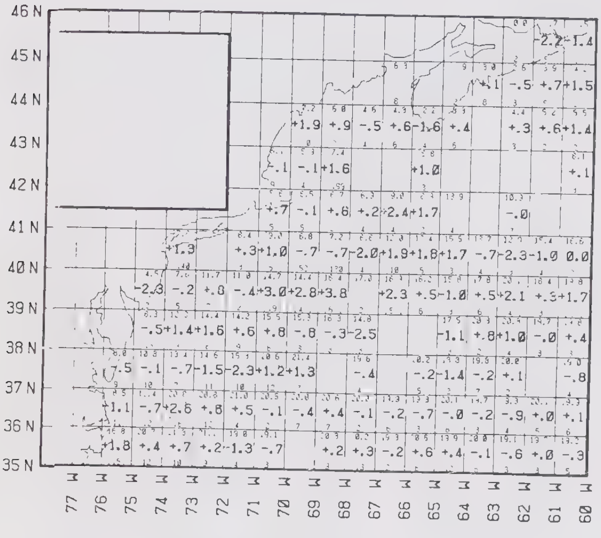

Figure 22. January 1980.

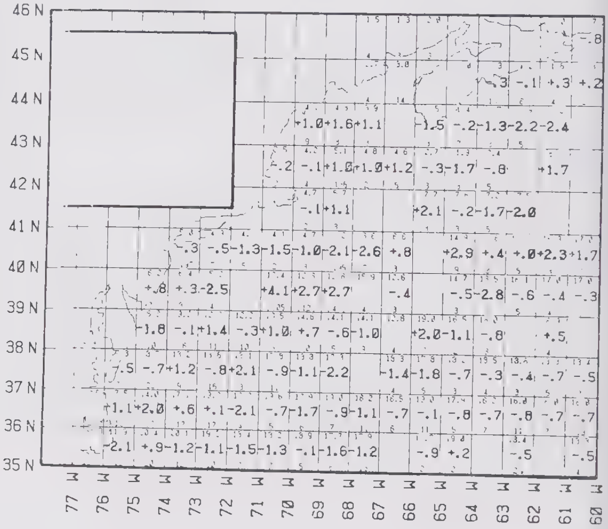

Figure 24. March 1980.

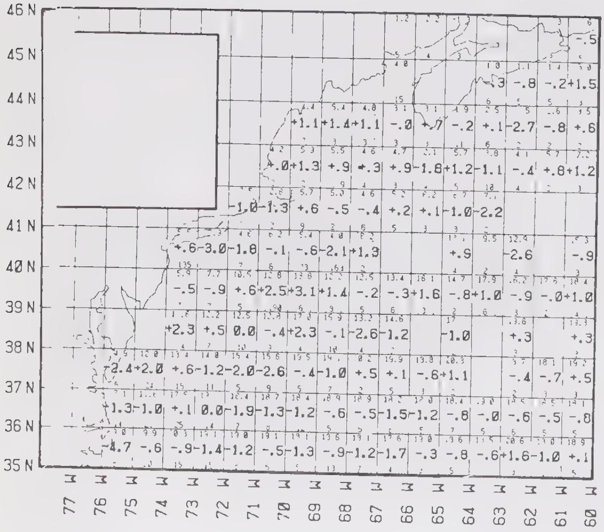

Figure 23. February 1980.

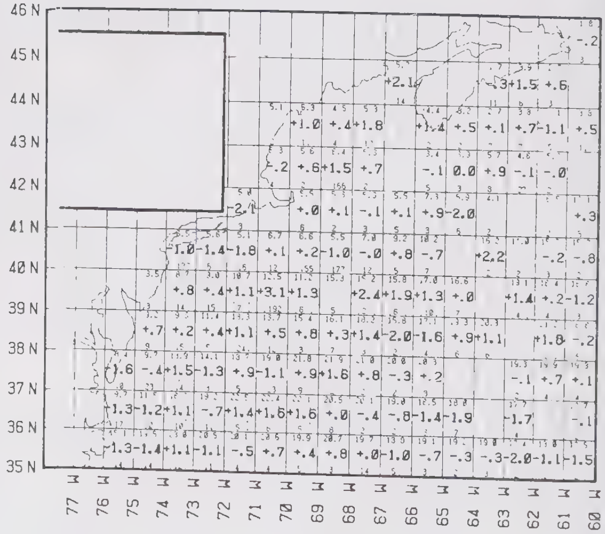

Figure 25. April 1980.

bservations are then printed in the 1° × 1° squares they naracterize to produce a map such as the one shown in igure 22. To facilitate interpretation of the data, nomalies greater than +1°C or less than −1°C are haded.

Monthly maps of this sort for the northwestern Atlanc for January 1980–January 1981 (Figs. 22–34) show hat distributions of SST anomalies were not very unusual until November, when Georges Bank (40°–42°N 66°–69°W) and the nearshore areas of the Middle Atlantic Bight showed strongly negative anomalies, as large as −3·1°C. This unusual cooling was the consequence of strong W–NW winds bringing cold, continental air into the New England and Middle Atlantic states and across coastal waters. Meteorological records from coastal weather stations for November (Table 4) clearly show the

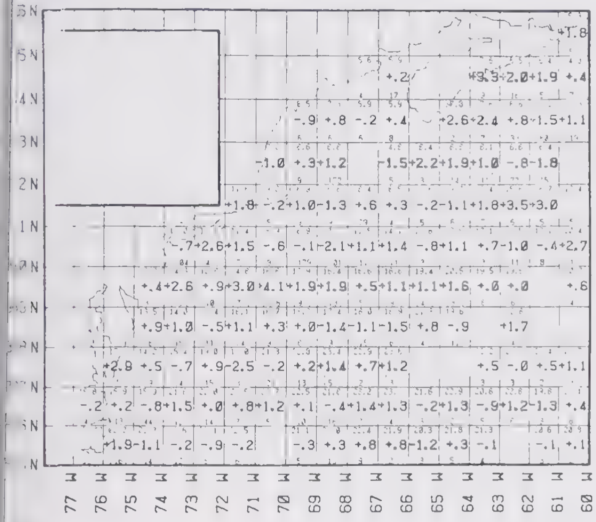

Figure 26. May 1980.

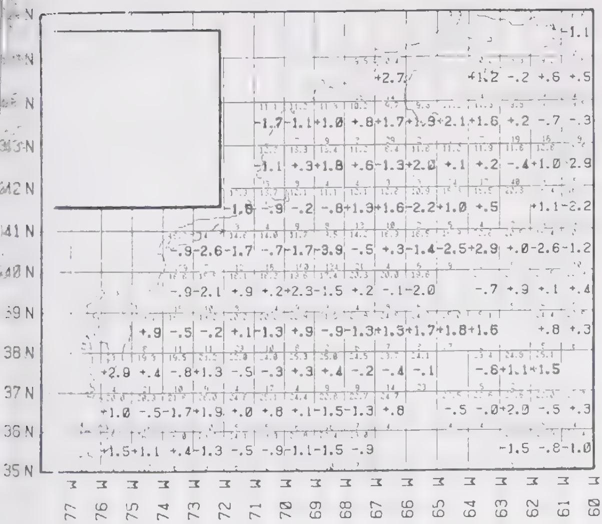

Figure 27. June 1980.

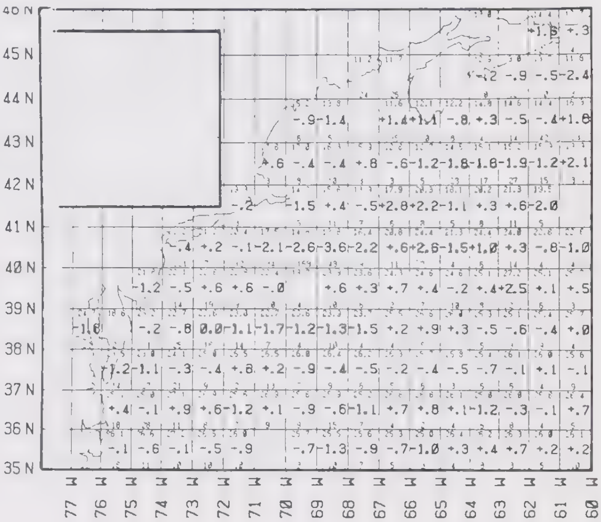

Figure 28. July 1980.

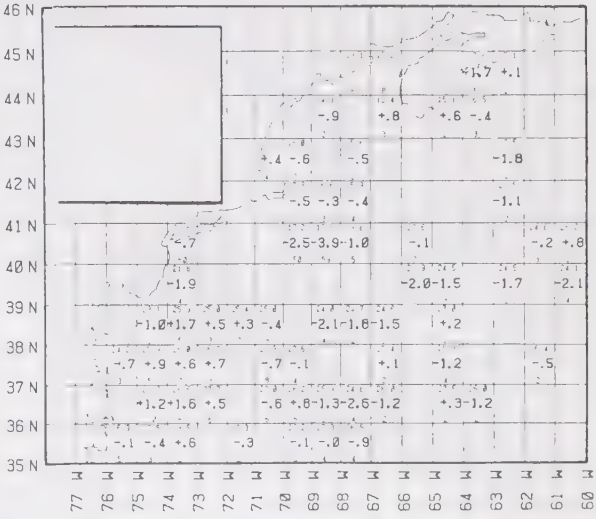

Figure 29. August 1980.

regional impact of the cold, continental air with temperature departures from normal ranging up to −2·6°C in Atlantic City.

The negative anomalies continued in the Georges Bank - Middle Atlantic Bight area during December 1980 and January 1981 as the result of a continuing westerly-northwesterly flow of cold air. January air temperatures were the most anomalous (Table 4) of the three months, but the negative SST anomalies were not noticeably greater then.

Pooled average SST anomalies for the entire mapped area (Table 5) similarly show the strongest negative anomalies in the November 1980 - January 1981 period. Otherwise the record is nearly featureless except for positive anomalies of 0·56 and 0·50 in May and September.

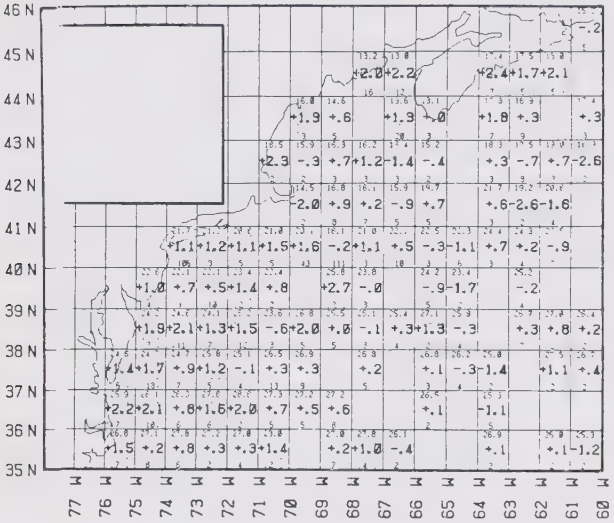

Figure 30. September 1980.

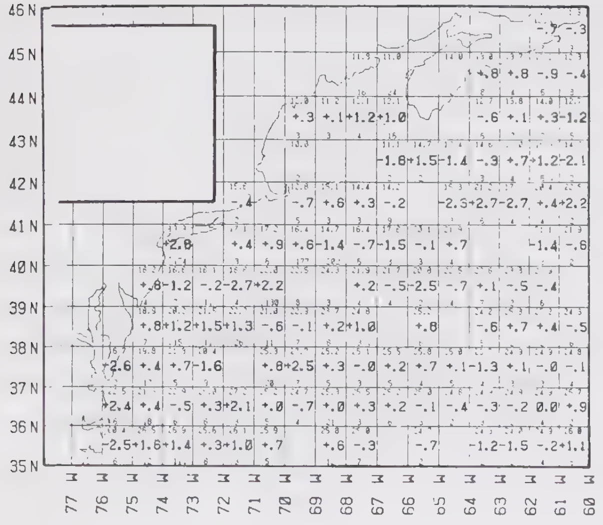

Figure 31. October 1980.

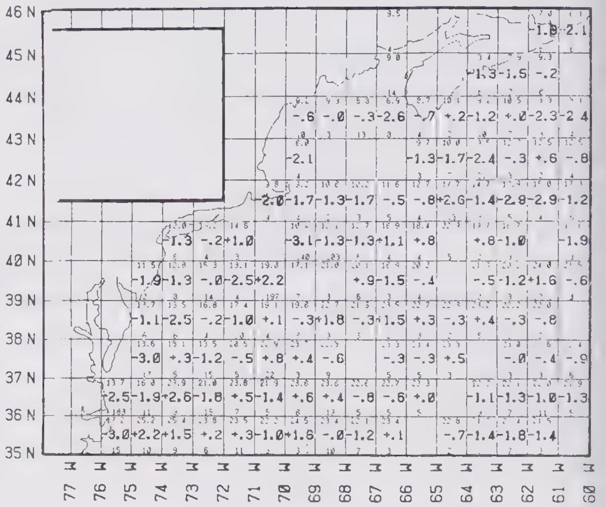

Figure 32. November 1980.

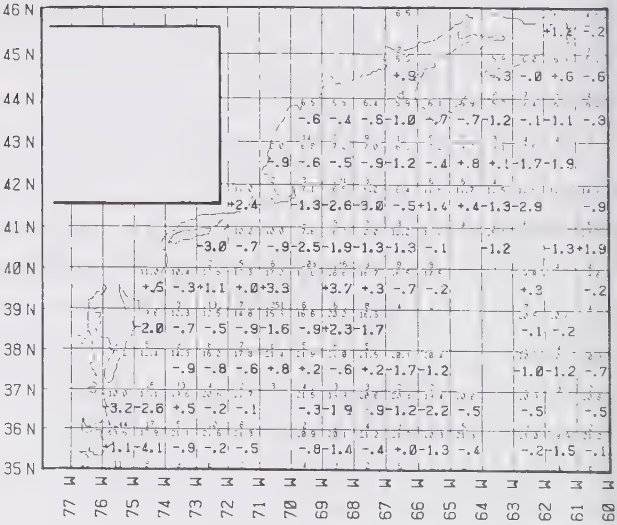

Figure 33. December 1980.

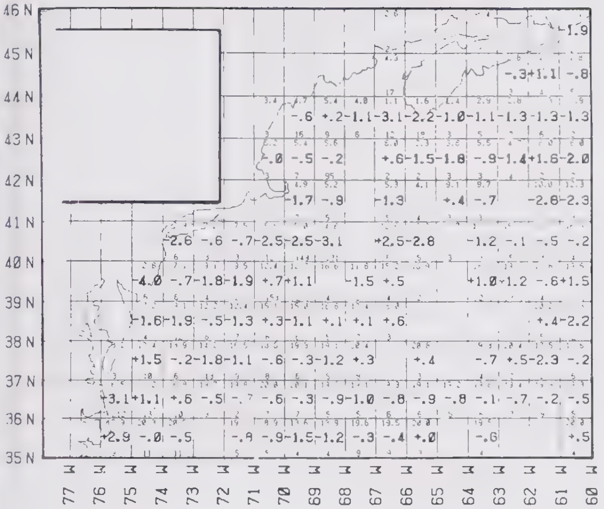

Figure 34. January 1981.

M. C. INGHAM
Atlantic Environmental Group, NMFS/NOAA
RR7, South Ferry Road
Narragansett, Rhode Island 02882, USA
D. R. MCLAIN
Pacific Environmental Group, NMFS/NOAA
c/o Fleet Numerical Oceanography Center
Monterey, California 93940, USA

AN OVERVIEW OF CALIFORNIA SQUID FISHERIES AND CALIFORNIA LIGHT FISHERY

BY

SUS KATO*

Pete and Jake asked me to talk about the California fishery and give a background on it. First I will give a little background of the fishery which started in Monterey about 1860 or so, which makes it about the oldest fishery on the West Coast. The Chinese were the first to fish squid. They used a two-boat purse seine which was about three fathoms deep and 30 fathoms long. They attracted the squid to the surface with a lighted torch. They didn't use much light, but they were pretty successful at it. The product was mainly dried and shipped to China and to Hawaii.

(Referring to a slide) I thought that I would show a slide of a squid. One can tell the male Loligo opalescens from the female mainly by the size of the head. The males always have bigger heads. The canning of squid started around 1920 and freezing in 1926. The bulk of the product was dried until about 1932 when the silver market collapsed, silver being used for payment. Something to do with the price of tea, I think. So the fishery kind of died down until about 1943 or so when it picked up again. This occurred mainly because we were shipping a lot of squid overseas. Right after the war a lot of it went to the Philippines and other places as part of our A.I.D. effort.

The Southern California fishery started around 1958 when they started getting more consistent catches. Here are some recent catch data. The Southern California fishery that started from scratch has just about caught up with Monterey. The total catch has steadily gone up. This reflects effort as well as an increase in market size, especially in Japan in recent years. A lot of squid is also going to Europe. Most of

* Chief of Underutilized Fisheries Resources Task Force, National Marine Fisheries Service, Tiburon, California. (415) 556-0565.

the catch is used frozen, some of it fresh, and about 20% is canned in any given year. These are the three main market forms of squid.

Fishing methods in Southern California and in Monterey are kind of different. The seasons are different as well. Most of the monthly catch in Monterey is made in May, June, and July. It is only during the spawning season that the squid are caught. In Southern California, most squid is caught in December, January, and February, except this year in which we haven't caught any squid yet.

The seasons are not the only things that are different. The catch methods are also different. In Monterey the lampara net, which is a round haul net, is exclusively used because they outlawed the purse seine in 1953. The lights, which are currently used in Southern California, were outlawed in 1959. These laws were actually put into effect by the industry.

The price also differs. Historically, Monterey has always paid higher prices for their squid -- presumably because the squid are better, but there are a lot of arguments about that. In 1981 the canners paid $115 a ton which is less than the $280 a ton price for freezer squid. At the same time the San Pedro price on freezer squid was $150 a ton and $90 a ton. This year, for the first time we just can't find any squid in Southern California, probably because of some funny weather conditions. Consequently the price has gone up to $400 a ton, which is the first time ever that the squid is more expensive in Southern California. This indicates that the quality of squid may not be that important.

I mentioned that light attraction is one way we catch squid in Southern California. We also use purse seines. Most boats are albacore boats that have a trolling rig on them and don't need much to get them ready for squid fishing. All you need are two 1500 watt incandescent lights up above, and two lights along the sides which are used to concentrate the squid. Then all you need is a big scoop. It is a simple method and very cheap, so a lot of people can get into the fishery. As I said before, most of the boats are albacore boats and fish squid in Southern California only in the winter.

The fishing locations are primarily Catalina, the Channel Islands and also on the coast. There are two canneries in San Pedro and one in Port Vanier and most of the freezing capacity is in San Pedro. They probably handle something like 250 tons per day now which is a lot more than the 100 tons per day that they processed a couple of years ago.

Most squid are caught in shallow water from 13-18 fathoms and because the boats have to anchor to catch squid with light, there is a limitation of about 35 fathoms due to the fact that you can't drop the hook in anything deeper. If you find any squid, which is the first problem, you should look for those predators which are feeding on dead and dying squid that come to the surface as they are spawning. The fishermen use the birds, pilot whales or sea lions to help them locate squid. They are good indicators of squid. Mostly they use a fathometer. The meters range from about 28 to 125 hertz. Only a couple of boats use sonar. At nighttime, illuminance is a good way to find them, especially if they are near the surface. After they find the squid at night they drop the hook, turn the lights on, and hope that they come up. They don't always. You have to judge whether the squid are going to come up or move to a different spot. This year everybody is apparently sitting on the squid and hoping they will come up. They sit on the squid for two or three days and they still don't come up. When you get enough squid under the light you can use a brail that is about 3-1/2 to five feet in diameter with a 12 foot handle. All you do is drop the brail in the water with a boom, pull it through the squid, and up it comes. Drain the water out and dump it in the hold. It is an effective method, and you can catch 40-50 tons at night with no problem. It seems like an easy job, but in actuality it is tough, hard labor.

Being a good government bureaucrat, I thought there was an easier way to make a living. A dozen years ago Matt May and I came up with this system called "squid slurp," which is almost the same as the brail method but uses a pump and a funnel in place of the brail. It really worked great. The pump was an eight-inch hydraulic capsule pump. We projected a wooden funnel about six feet wide out from it and put on another underwater lamp right above the funnel. The rest of the gear was comprised of a separator screen which sent the water over the sides and shot the squid right into the hold. One night we caught about 70 tons while drinking coffee. Matt made some changes on this thing, and it really works much better now. Later, we took off the top panel to avoid the surge which we found to be a big problem during rough weather. If we put this pump right under the tracking lamp, we also found that we didn't need an underwater lamp.

QUESTION: How much does this unit weigh?

KATO: Probably three-quarters of a ton. The pump has some disadvantages. When the squid are dead on top of the water they don't move, and it is very tough to pump squid under those conditions. When they are alive and moving we get 15 tons in 10 minutes, but in other cases when they are not moving, to scoop is actually faster. Also this pump will damage maybe two to five percent of the heads of the squid so the freezers don't care for it too well. In rough weather it is pretty tough to work, although we did okay in about 30-knot winds. Unloading is done mainly by brail which takes a lot of time. This is one of the reasons why you need a crew. The pump is not that advantageous when you are unloading. It is very simple; the squid are loaded in boxes and go into slush ice directly at the freezer plant. At the canneries they use fish pumps, making it much easier and faster.

The second method used in Southern California is the purse seine. They find the squid in much the same way the light boats do, but most of these boats use sonar so they can find the fish better. And they fish in the same grounds as the light boats. Matt doesn't like it because he thinks they are dredging up the eggs, which there may be some truth to. About 10-15 boats fish seines. A half dozen of them fish steadily and this is mainly dictated by the market. If the market asks the boats to fish, they will go out and get squid because they are valuable now. In the light fishery we get anywhere from 20-70 boats, which also depends on the market conditions.

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ЗООЛОГИЧЕСКИЙ ЖУРНАЛ

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ОСНОВНЫЕ ЧЕРТЫ ФОРМИРОВАНИЯ КОСТНОГО ЧЕРЕПА ДЕЛЬФИНОВ (CETACEA) В ПРЕНАТАЛЬНЫЙ ПЕРИОД

А. А. КУЗЬМИН, У. Ф. ПЕРРИН

Приведены данные о формировании костного скелета головы косатки, дельфина-белобочки, пятнистого и длиннорылого продельфинов в пренатальный период. Отмечено значительное сходство в развитии черепа этих видов, что служит еще одним доказательством высказанного ранее в литературе мнения о монофилетическом происхождении зубатых китов. Формирование костей крыши черепа дельфинов и кашалота подвержено индивидуальной и межвидовой изменчивости и выявляет признаки сходства со звероподобными рептилиями. Впервые подробно описаны закладка и формирование подбородочно-меккелевой кости у зубатых китообразных. Дискутируется вопрос о гомологизации покровных костей крыши черепа зубатых китов.

По мнению ряда исследователей (Miller, 1923; Howell, 1930; Слепцов, 1968 и др.), перекрытие одних костей другими возникло в черепе зубатых (Odontoceti) и усатых (Mysticeti) китов параллельно. На основании результатов палеонтологических исследований Мчедлидзе (1970, 1976) считает, что телескопия черепа у этих китообразных — явление конвергентное. С последним согласуются и данные сравнительного изучения эмбриогенеза скелета головы кашалота (*Physeter macrocephalus*) и полосатиков — Balaenopteridae (Кузьмин, 1976, 1978). Не только в этом вопросе, но и по поводу гомологизации костей мозгового отдела черепа и причин возникновения значительных различий, характерных для строения черепа взрослых зубатых и усатых китов, мнения исследователей расходятся (Ridewood, 1922; Slijper, 1936; Слепцов, 1940; Яблоков, 1964; Кузьмин, 1974, 1975, 1976; Kuzmin, 1976 и др.).

В целях выяснения особенностей строения черепа зубатых и усатых китов необходимо тщательное изучение его развития в пренатальный период у множества видов. Это также имеет важное значение для дальнейшей разработки представлений об эволюции китообразных и уточнения их систематического положения.

В настоящее время среди видов зубатых китов эмбриогенез костного черепа изучен, по-видимому, наиболее полно у кашалота (Кузьмин, 1969, 1974, 1975, 1976, 1978, 1979; Kuzmin, 1976; Берзин, 1971; Блохин, 1972), дельфина-белобочки (*Delphinus delphis*), белухи (*Delphinapterus leucas*) и морской свиньи (*Phocoena phocoena*) (Слепцов, 1939, 1940, 1968). Подробно описан хрящевой скелет беломордого дельфина (*Lagenorhynchus albirostris*), гринды (*Globicephala melaena*) и морской свиньи (Burlet, 1913, 1913a; Schreiber, 1916).

В настоящей статье приведены новые данные по эмбриогенезу костного скелета головы косатки (*Orcinus orca*), дельфина-белобочки, пятнистого (*Stenella attenuata*) и длиннорылого (*St. longirostris*) продельфинов в сравнении с другими зубатыми китами. Цель исследования — выявить характерные черты строения краниального скелета, особенности изменений общей конфигурации черепа и топографии его элементов у дельфинов и пренатальный период и оценить возможность использования полученных данных в целях изучения эволюции этих животных и их внутривидовой структуры.

МАТЕРИАЛ И МЕТОДИКА

Изучен костный скелет головы эмбрионов следующих видов: *St. attenuata* — 9♂♂ (98, 125, 155, 203, 260, 310, 320, 405, 505)[1], 2♀♀ (635, 870[2]); *St. longirosris* — 5♂♂ (95, 205, 390, 518), 2♀♀ (209, 728); *D. delphis* — 3♀♀ (280, 360, 498); *O. orca* — ♀ (180), ♂ (1530).

Кроме указанных материалов, использованы данные по топографии покровных костей черепов дельфинов, полученные в результате исследований остеологических коллекций китообразных в музеях Зоологического института АН СССР (Ленинград) и Московского университета.

Материалы обработаны в лабораториях Тихоокеанского научно-исследовательского института рыбного хозяйства и океанографии и Юго-Западного центра рыбохозяйственных исследований США. Эмбрионы мелких дельфинов собраны на рыболовных судах США в восточной части тропической зоны Тихого океана.

Препараты черепа приготовлены методами заливки его полости парафином (Кузин, 1975) и мацерации в воде (Заславский, 1966). Сведения по онтогенезу скелета головы кашалота, приводимые в разделе «Результаты исследований», взяты из работ Кузьмина (1974, 1975, 1976, 1978, 1979).

РЕЗУЛЬТАТЫ

Степень окостенения и общая конфигурация черепа у исследованных нами самых мелких одноразмерных эмбрионов пятнистого и длиннорылого продельфинов оказались неодинаковыми: у пятнистого мозговой отдел имел менее округлую форму, рострум был относительно шире, очаги костной ткани в элементах были крупнее; черепная коробка имела бо́льшие размеры у длиннорылого (рис. 1). У эмбриона пятнистого продельфина между верхнезатылочной и межтеменной костями находились два очага окостенения, а у эмбриона длиннорылого — к верхнезатылочной кости прилежал участок костной ткани иной конфигурации и не было окостенения в межтеменной кости (рис. 1). Нижнечелюстная кость окостенела у этих эмбрионов довольно полно. По всей ее длине проходил меккелев хрящ. В черепе сравниваемых эмбрионов были хорошо выражены признаки асимметрии и телескопии (верхнечелюстные кости налегали на лобные).

Существенные различия наблюдаются в окостенении скелета головы пятнистого и длиннорылого продельфинов и на последующих стадиях эмбриогенеза. Так, в черепе эмбриона пятнистого продельфина длиной 155 мм, в отличие от черепа эмбриона длиннорылого продельфина длиной 205 мм, кости в крыше черепа прилежали друг к другу плотнее, верхнечелюстные сильнее перекрывали лобные, а носовые были крупнее (рис. 2). В черепе эмбриона длиннорылого продельфина дорсальная часть верхнезатылочной кости имела форму крыльев. Между ними и межтеменной костью находилась фонтанель, которая у изученных нами видов дельфинов в основном закрывается за счет разрастания окружающих ее костей, но иногда на ее месте закладывается непарный костный элемент (рис. 2, *11*). Учитывая это, а также своеобразную конфигурацию верхнезатылочной кости у ранних эм-

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[1] В скобках — значения зоологической длины исследованных экземпляров, мм.

[2] Новорожденный.

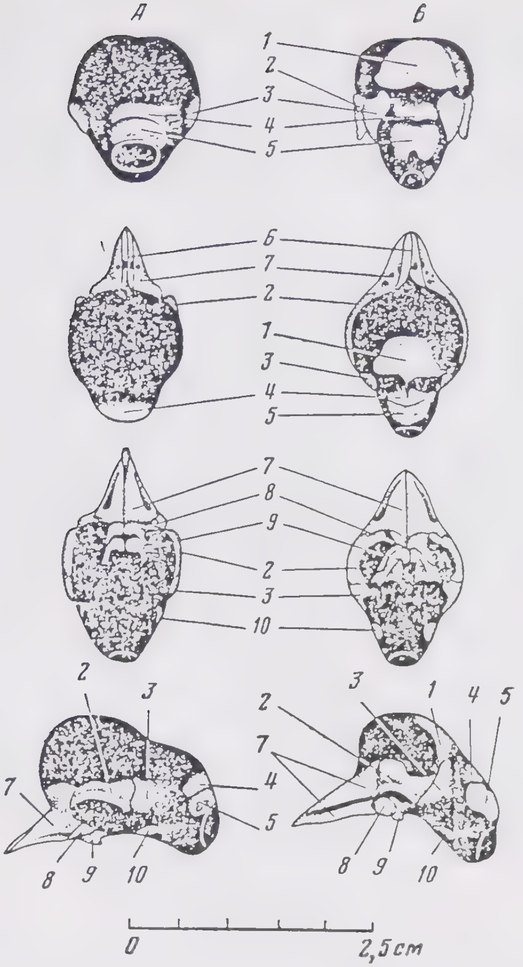

Рис. 1. Череп эмбрионов продельфинов: *А* — длиннорылого длиной 98 мм, *Б* — пятнистого длиной 95 мм; *1* — межтеменная кость, *2* — лобная, *3* — теменная, *4* — таблитчатая, *5* — верхнезатылочная, *6* — межчелюстная, *7* — верхнечелюстная, *8* — нёбная, *9* — крыловидная, *10* — височная

брионов косатки, пятнистого и длиннорылого продельфинов, мы полагаем, что у них, как и у белухи и морской свиньи (Слепцов, 1940), в затылочной области черепа, кроме верхнезатылочной и межтеменной, закладываются парная и непарная кости. Эти кости встречались в черепе не каждого эмбриона одного и того же вида: чаще парная кость наблюдалась у эмбрионов с длиной тела до 200 мм, а непарная оставалась иногда самостоятельной до середины пренатального периода (рис. 3).

Для ранних стадий эмбриогенеза черепа длиннорылого и пятнистого продельфинов оказалась характерна не только межвидовая, но и индивидуальная изменчивость. Межвидовая проявляется в своеобразии формирования общей конфигурации черепа, интенсивности его окостенения, форме и топографии элементов, индивидуальная — в числе и конфигурации костей, формирующих заднюю и верхнюю стенки черепной полости.

У изученных эмбрионов косатки, продельфинов и кашалота в элементах крыши черепной коробки костная ткань разрастается из центров окостенения по радиальному типу в следующей последовательности: в лобных — спереди назад и снизу вверх; в теменных — вверх и назад; в межтеменном — вперед и в стороны.

По данным Слепцова (1940), у белухи, дельфина-белобочки и морской свиньи межтеменная кость окостеневает из двух центров, которые не срастаются продолжительное время. Учитывая это, мы детально изучили строение межтеменной кости в черепе всех имевшихся у нас

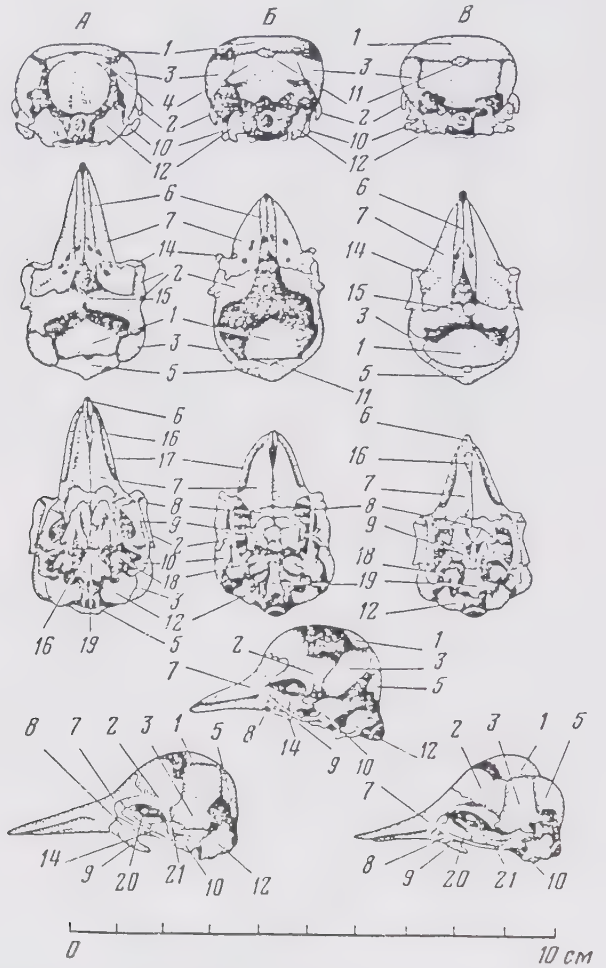

Рис. 2. Череп эмбрионов дельфинов: *А* — длиннорылого продельфина длиной 205 мм, *Б*—косатки длиной 180 мм, *В* — пятнистого продельфина длиной 155 мм; *11* — кожная верхнезатылочная, *12* — боковая затылочная, *14* — скуловая, *15* — носовая, *16* — сошник, *17* — зубной канал верхнечелюстной кости, *18* — барабанная, *19* — основная затылочная, *20* — орбитосфеноид, *21* — алисфеноид; остальные обозначения как на рис. 1

эмбрионов продельфинов, косатки и дельфина-белобочки. Признаков, указывающих на возможность образования у них межтеменной кости из двух очагов окостенения, нам выявить не удалось.

Теменной родничок в черепе эмбрионов пятнистого и длиннорылого продельфинов закрывается при длине тела 200—300 мм. У косатки и дельфина-белобочки он зарастает также рано. На последующих стадиях эмбриогенеза у этих дельфинов верхняя и боковые затылочные кости наползают постепенно на теменные и межтеменной элементы, что определяет своеобразные изменения их конфигурации (см. рис. 1—3). Происходит изменение общей конфигурации черепа, однако существенных различий, связанных с возрастом, в его боковом профиле у продельфинов и дельфина-белобочки нет.

По нашим данным, сосцевидные роднички в черепе косатки, дельфина-белобочки и пятнистого продельфина закрываются только после рождения. Это характерно и для развития скелета головы карликовой косатки (*Feresa attenuata*) (Perrin, Hubbs, 1969). У длиннорылого продельфина они зарастают к концу эмбриогенеза, у кашалота — в начале второй половины этого периода. В исследованном нами черепе новорожденного пятнистого продельфина (длина тела 870 мм) в сосцевидных родничках находились маленькие косточки: в правом — три, в левом — две. Эти кости описаны у тюленей и их обычно считают «дополнительными» затылочными или фонтанельными (Howell, 1929; Doutt, 1942; King, 1956; Morejohn, Briggs, 1973 и др.). В черепе этого же новорожденного продельфина в верхнезатылочной кости на 15 мм выше затылочного отверстия находились два элипсовидных отверстия. Они были удалены друг от друга на 17 мм. Правое имело размеры 9×5 мм, левое — 11×8 мм. В черепе остальных исследованных нами эмбрионов дельфинов и кашалота этих отверстий не было.

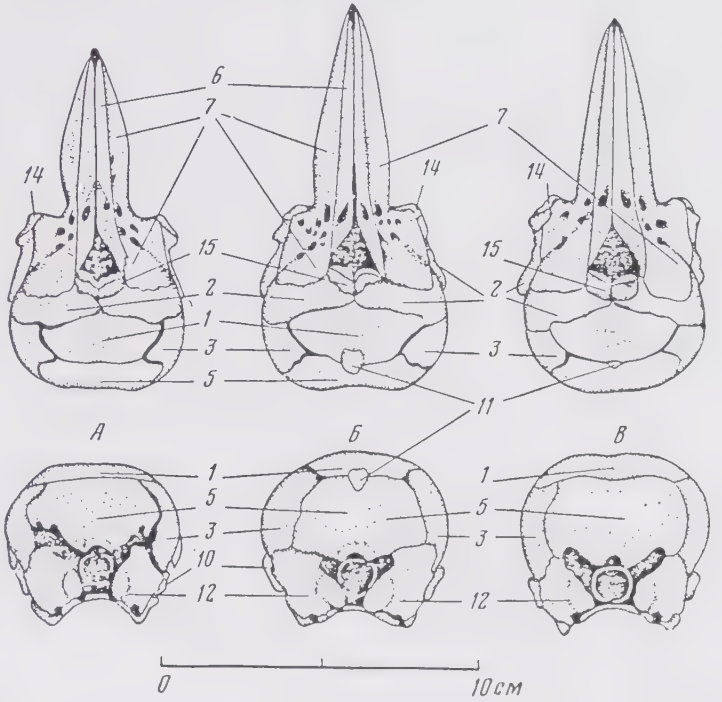

Рис. 3. Череп эмбрионов дельфинов: *А* — дельфина-белобочки длиной 280 мм; *Б* — длиннорылого продельфина длиной 304 мм; *В* — пятнистого продельфина длиной 310 мм; обозначения как на рис. 1 и 2

По нашим данным, как в правой, так и в левой половинах черепа пятнистого продельфина надглазничных отверстий бывает от трех до семи, чаще пять, у длиннорылого продельфина — от трех до семи, у дельфина-белобочки от трех до шести. Возрастной изменчивости эти признаки не подвержены. Видимо, они — проявление эпигенетического полиморфизма и могут быть использованы для изучения внутривидовой структуры указанных дельфинов, как это раньше было показано для наземных млекопитающих и ластоногих (Яблоков, 1966; Тимофеев-Ресовский и др., 1973 и др.).

В эмбриогенезе наибольшего развития гребни в крыше черепа достигают у кашалота. К моменту рождения их формирование находится на начальных стадиях. У мелких дельфинов наружная поверхность черепной коробки остается гладкой в течение всего эмбриогенеза.

Закладку слезных костей у продельфинов мы не обнаружили. Вполне возможно, что они у этих китообразных, как и у кашалота, очень рано сливаются со скуловыми костями, окостенение которых у продельфинов начинается спереди, и вскоре соединяются со скуловым отростком височной кости. Крыловидный отросток чешуи височной кости, разрастаясь, полуохватывает с латеральной стороны и спереди барабанную кость. У эмбрионов продельфинов длиной 250—300 мм он достигает крыловидной кости. Последняя у зубатых китов имеет сложную конфигурацию. По нашим данным, у эмбрионов продельфинов этих же размеров она уже соединяется с лобной, нёбной, сошником и основной затылочной костями и налегает на вентральные поверхности алисфеноида и орбитосфеноида. Возрастные изменения топографии нёбных и крыловидных костей имеют у изученных дельфинов видовую специфичность, выражающуюся главным образом в их форме и размерах в течение всего эмбриогенеза.

Сошник у эмбрионов продельфинов длиной 130—150 мм просматривается со стороны костного нёба. У эмбрионов этих дельфинов длиной 200—250 мм он плотно прилежит к пресфеноиду и базисфеноиду, и его каудальный край уже достигает основной затылочной кости (рис. 2). В отличие от кашалота, сошник у дельфинов не доходит до конца рострума на $^1/_3$ длины.

Начальные стадии окостенения барабанных костей проявляются у изученных нами продельфинов при длине тела эмбрионов около 120 мм. Их костные участки в этот период развития по форме напоминают полумесяц, обращенный вогнутым краем в сторону основной затылочной кости. Молоточек формируется у дельфинов за счет окостенения каудальной части меккелева хряща. У эмбрионов пятнистого и длиннорылого продельфинов длиной 200—300 мм к молоточку прилежит кожно-сочленовая кость, которая на последующих стадиях развития сливается с молоточком, а молоточек — с сигмовидным отростком барабанной кости. У эмбрионов этих дельфинов длиной 350—400 мм стремя довольно прочно соединено с каменистой костью, составные части которой уже жестко прикреплены друг к другу и к прилежащим к ним костям черепа. В отличие от мелких дельфинов, у косатки формирование слуховых костей проходит менее интенсивно. Так, у ее эмбриона длиной 1530 мм все слуховые косточки были свободными, а составные части каменистой кости легко отделялись друг от друга и от костей черепа. Это характерно и для кашалота.

По нашим данным, у эмбриона косатки длиной 180 мм между барабанной, основной и боковой затылочными костями находился очаг окостенения удлиненной формы (рис. 2). На этом месте в черепе эмбриона пятнистого продельфина длиной 125 мм был участок костной ткани округлой формы. Мы не смогли определить скелетогенную основу этих очагов окостенения. В ходе развития они очень быстро сливаются с окостеневшей частью основной затылочной кости и образуют расширение ее каудального конца в виде крыльев. Одновременно происходит разрастание в ширину ее переднего конца. Отмеченные возрастные изменения конфигурации основной затылочной кости у дельфинов в эмбриогенезе свойственны и кашалоту, однако подобных «дополнительных» очагов окостенения в основании его черепа не наблюдается.

Базисфеноид и пресфеноид у косатки, пятнистого и длиннорылого продельфинов, как и у кашалота, формируются из трех центров окосте-

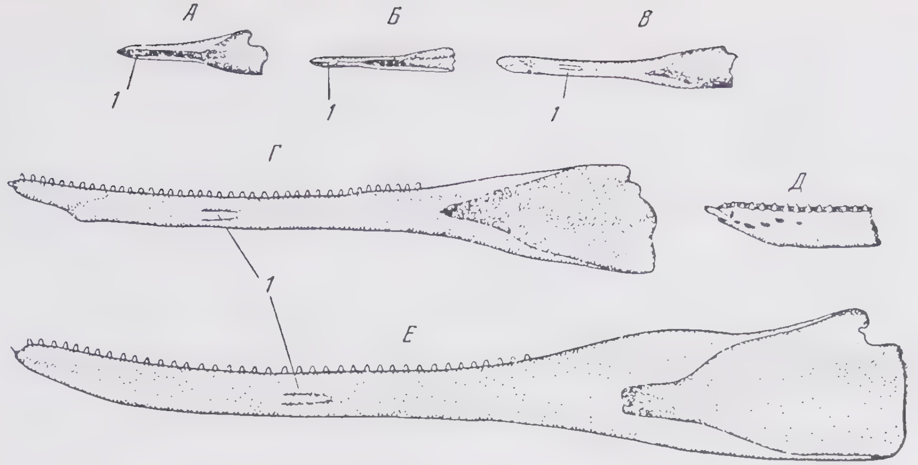

Рис. 4. Строение нижнечелюстной кости эмбрионов дельфинов: *А* — косатки длиной 180 мм; *Б* — пятнистого продельфина длиной 180 мм; *В* — то же, что *Б*, длиной 260 мм; *Г* и *Д* — то же, что *Б* и *В*, длиной 631 мм; *Е* — новорожденного пятнистого продельфина длиной 870 мм; *1* — подбородочно-меккелева кость

нения. Очаги окостенения сливаются в передней и основной клиновидных костях у продельфинов при длине тела эмбрионов 300—350 мм, а базисфеноид и пресфеноид не срастаются друг с другом в течение всего эмбриогенеза.

У косатки, дельфина-белобочки, пятнистого и длиннорылого продельфинов закладывается подбородочно-меккелева кость (рис. 4). Она образуется путем перихондрального окостенения переднего конца меккелева хряща. С увеличением возраста эмбрионов подборочно-меккелева кость у этих китов перемещается с переднего конца нижнечелюстной кости к ее середине. У косатки и продельфинов в эмбриогенезе нижнечелюстная кость формируется почти одинаково. Различие в том, что у продельфинов и дельфина-белобочки на переднем конце как левой, так и правой нижнечелюстной кости имеется один длинный зуб, вершина которого направлена вперед. Этот зуб в ходе развития постепенно обрастает костной тканью. У предродовых эмбрионов он находится внутри нижнечелюстных костей. Выявленное нами смещение подборочно-меккелевой кости и обрастание переднего нижнечелюстного зуба костной тканью у дельфинов в эмбриогенезе, по нашему мнению, свидетельствуют об интенсивном увеличении в длину челюстных костей у этих китов на последних этапах эволюции.

У изученных нами дельфинов тело и гортанные рога предъязычной кости окостеневают из единой хрящевой основы, что характерно и для кашалота. Язычные рога этой кости у них не окостеневают вообще, а из члеников дорсальной ветви окостеневает только средний. Его проксимальный конец остается хрящевым на протяжении всего онтогенеза.

Таким образом, выполненные исследования по эмбриогенезу костного черепа дельфинов показали, что у них как и у кашалота, закладываются и развиваются все основные костные компоненты осевого скелета головы млекопитающих в целом. Однако эмбриогенез их черепа, в отличие от наземных млекопитающих и ластоногих, имеет следующие особенности: не окостеневает решетчатый элемент, в меньшей степени выражено слияние каменистой кости с височной и боковой затылочной, закладываются подбородочно-меккелева кость и большее число покровных костей в черепной коробке, развиваются мощные асимметрия и телескопия черепа.

ОБСУЖДЕНИЕ

По мнению Слепцова (1940), сравнительные анатомы ошиблись в гомологизации костей крыши черепа дельфинов, приняв теменную за межтеменную, а заднелобную — за теменную. Он в основном опирался на оригинальные данные исследований эмбриогенеза черепа белухи, дельфина-белобочки и морской свиньи. У них, а по нашим материалам, и у косатки, пятнистого и длиннорылого продельфинов, закладываются парный и непарный костные элементы между верхнезатылочной, межтеменной и теменными костями. По нашим данным, парный очаг окостенения в черепе дельфинов, закладывающийся сразу же впереди верхнезатылочной кости, в ходе развития разрастается влево и вправо и сливается с ней без видимых следов шва (рис. 1—3). Много сходных черт с дельфинами проявляется и в ходе формирования верхнезатылочной кости у кашалота (Кузьмин, 1975; Kuzmin, 1976). Выявленные особенности начальных стадий развития затылочной области черепа у зубатых китов, несомненно, свидетельствуют о том, что в черепе их предков к переднему краю верхнезатылочной кости примыкал парный костный элемент.

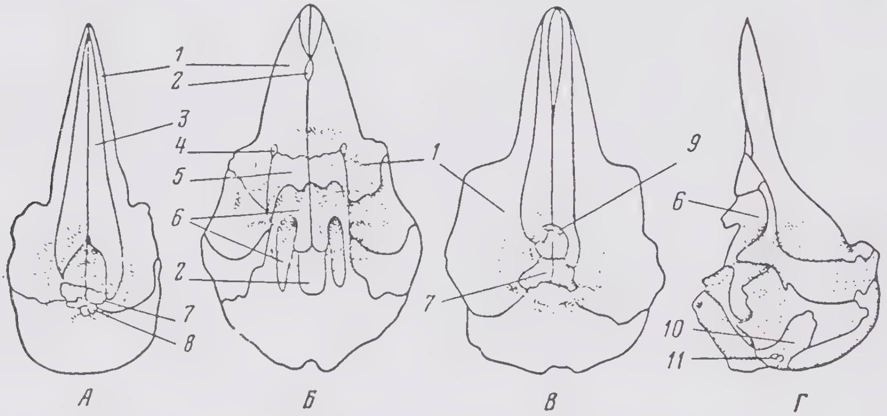

Рис. 5. Череп взрослых дельфинов: *А* — афалины; *Б* и *В* — морской свиньи; *Г* — афалины; *1* — верхнечелюстная, *2* — сошник, *3* — межчелюстная, *4* — «преднёбная», *5* — нёбная, *6* — крыловидная, *7* — носовая, *8* — межтеменная, *9* — возможно, рудименты решетчатой, *10* — надвисочная, *11* — дополнительные (фонтанельные) затылочные

У ископаемых пресмыкающихся к дорсальному краю верхней затылочной кости прилегали кожные верхнезатылочные кости (Ромер, 1939; Рождественский, 1964; Шмальгаузен, 1964 и др.). К их латеральным краям присоединялись таблитчатые кости, а впереди кожных верхнезатылочных, которые в сравнительно-анатомических обзорах обозначаются как заднетеменные (Кингсли, 1914; Шмальгаузен, 1947 и др.), у древних наземных позвоночных находился парный теменной элемент. В черепе звероподобных рептилий, например циногнатуса, таблитчатые кости соединялись с непарной кожной верхнезатылочной костью и в виде широких крыльев окружали с боков и сверху почти всю верхнезатылочную кость (Ромер, 1939). При сравнении особенностей возрастных изменений конфигурации верхнезатылочной кости у зубатых китов в эмбриогенезе (Кузьмин, 1975, 1976) (рис. 1—3) и строения черепа звероподобных рептилий прослеживается топографическое сходство.

У изученных дельфинов и белухи межтеменная кость не сливается с прилежащими элементами и в ходе развития перемещается вперед к лобным костям (Слепцов, 1939, 1949) (рис. 1—3). В одном черепе взрослых афалин из 78 изученных нами межтеменная кость была парной (рис. 5). В связи с этим вполне возможно, что неоднократно описанные в лобной области черепа млекопитающих «дополнительные» кости (Doutt, 1942; Westoll, 1943; Hromada, Strand, 1962 и др.) и межтеменная кость у дельфинов — гомологи одних и тех же костей ископаемых позвоночных. Кроме того, изучая скелет головы взрослых афалин, в одном из них мы обнаружили «дополнительную» парную кость. Она граничила с теменной, боковой и верхней затылочными и височной костями — местоположение, характерное для надвисочной кости ископаемых пресмыкающихся (рис. 5). Таким образом, теменная кость в черепе дельфинов, видимо, — сложное образование, в состав которого в процессе эволюции влились межвисочный и надвисочный элементы, а возможно, и тот и другой ископаемых позвоночных. Наблюдаемое иногда разделение правой теменной кости у кашалота в эмбриогенезе (Кузьмин, 1975, 1976; Kuzmin, 1976) позволяет предполагать, что у него в эволюции теменные элементы слились с височными или заднелобными костями.

Доказательством высказанного предположения может служить следующее: центры окостенения в теменных костях высших зверей появляются у их основания и затем разрастаются по радиальному типу, в основном вверх (Бирих, 1957; Третьяков, 1959; Jollie, 1968; Кузин, 1970; Кузьмин, 1975, 1976; Kuzmin, 1976) (рис. 1—2).

Исходя из вышеизложенного, мы полагаем, что встречающийся у разновозрастных эмбрионов дельфинов непарный костный элемент между верхнезатылочной и межтеменной костями является гомологом кожного верхнезатылочного элемента древних рептилий. Кость, обозначенная на наших рисунках у дельфинов как межтеменная (рис. 1—3) и описанные в лобной области черепа млекопитающих «дополнительные» кости, видимо, — гомологи одних и тех же костей древних позвоночных. Закладывающийся впереди верхнезатылочной кости в черепе дельфинов парный элемент — гомолог таблитчатых костей вымерших рептилий. Теменная кость у зубатых китов — сложное образование, сформировавшееся в процессе эволюции из элементов теменной и височной областей черепа ископаемых животных.

В работах Слепцова (1939, 1940) и Агаркова и др. (1974) упоминается наличие в черепе дельфинов решеточной кости. По данным Бурле (Burlet, 1913, 1913a), у морской свиньи она не окостеневает вообще. Это характерно и для онтогенеза черепа кашалота, косатки, пятнистого и длиннорылого продельфинов и дельфина-белобочки (Кузьмин, 1975, 1976; Kuzmin, 1976) (рис. 1—3). В черепе взрослых кашалотов со стороны рострального углубления хорошо виден гребень пресфеноида, а у дельфинов он скрыт под лобными костями. Костная стенка между носовыми проходами у взрослых дельфинов образована слившимися между собой боковыми пластинками сошника. В связи с этим представляет интерес наличие в черепе некоторых особей белокрылой и обыкновенной морских свиней маленьких самостоятельных косточек, находящихся впереди костных хоан (рис. 5). Вполне возможно, что парная кость, обнаруженная нами в черепе взрослых особей двух видов дельфинов, — рудимент решетчатой кости.

Особенности развития скелета головы зубатых китов в начале онтогенеза (Кузьмин, 1975, 1976; Kuzmin, 1976) (рис. 1—3) позволяют сомневаться в наличии прямой связи между современными зубатыми китами и древними китообразными (Archeoceti). Об этом свидетельствует отсутствие у археоцет подбородочно-меккелевой кости, характерной для эмбриогенеза черепа дельфинов, и пятой кости в затылочном элементе, которая у новорожденных кашалотов не сращена с боковой, основной и верхнезатылочной костями (Кузьмин, 1975, 1976; Kuzmin, 1976) (рис. 4). Подбородочно-меккелева кость не описана и у звероподобных рептилий. Однако не исключено, что при изучении фоссилизированных остатков звероподобных рептилий меккелева кость могла остаться у них невыявленной. Поэтому, какие бы сейчас предположения ни выдвигались, очевидно пока следующее: в эмбриогенезе зубатых китов проявляются признаки, сходные с элементами строения черепа звероподобных рептилий.

Выполненное нами обобщение сведений по эмбриогенезу костного скелета головы кашалота, косатки и мелких дельфинов (Слепцов, 1939, 1940; Кузьмин, 1969—1976; Kuzmin, 1976) (рис. 1—4) показало, что их череп в этот период развития характеризуется многими общими признаками. Главные из них — налегание каудальных отделов верхнечелюстных костей на лобные, хорошо выраженная закладка таблитчатых и кожных верхнезатылочных костей, открытая глазница, большое сходство в формировании затылочного и крыло-клиновидного комплексов и отсутствие окостенения в решетчатой кости. Это, несомненно, — серьезное подтверждение уже сложившегося мнения исследователей о монофилетическом происхождении современных зубатых китов.

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ТИНРО (Владивосток), Юго-Западный
центр рыбохозяйственных исследований
США (Ла-Холья, Калифорния)

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THE MAIN FEATURES OF THE SKULL FORMATION IN DOLPHINS (CETACEA) DURING THE PRENATAL PERIOD

A. A. KUZ'MIN, W. F. PERRIN

Pacific Research Institute of Fisheries and Oceanography (Vladivostok)
and Southwest Fisheries Center (La Jolla, California, USA)

Summary

The data are provided on skull formation in the killer whale, common dolphin, spotted dolphin and long-snout dolphin during the prenatal period. A marked similarity in the skull development of these species serves as one more evidence of the previously forwarded suggestion on monophyletic origin of toothed whales. The formation of skull vault bones in dolphins and sperm whale is subject to individual and interspecific variation and is similar with that in the Theromorpha. The origin and formation of the mentomeckelian bone is first described in detail for the toothed whales. The problem of homologization of the skull vault bones in the toothed whales is discussed.

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New Ideas on the Fluctuations of the Clupeoid Stocks off California

REUBEN LASKER[1]

National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038, USA

AND ALEC MACCALL

California Department of Fish and Game, c/o Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038, USA

Fisheries scientists have been intrigued with the boom and bust phenomenon that characterizes many fisheries but is particularly exemplified by the clupeoid fisheries, i.e. sardine, anchovy, menhaden, herring. Some of the clupeoids achieve huge populations with biomasses in the millions of tons. Exploitation by coastal nations is for human and animal food, the latter by a reduction of fish to meal which is usually included in diets of poultry and cattle to provide essential amino acids for protein metabolism and growth. Many nations have suffered the economic and social distress of industrial failure due to the collapse of a mainstay clupeoid fishery. Today the clupeoids make up about one-third of the world's fish catch. However, between 1968 and 1971 the catch of the Peruvian anchoveta averaged 10 million t per year and alone contributed 15% of the world fish catch. Figure 1 illustrates the precipitous decline of the Peruvian anchoveta (*Engraulis ringens*) catch and some of its related consequences, for example the rise in the cost of fish meal on the world's markets and the substitution of soybean (another protein source) for fish meal.

California coastal fisheries in the late 1930s and through the 1940s rode the economic boom of a thriving sardine (*Sardinops sagax*) fishery. Catches of this species for all California ports totalled as much as 658 000 t in the 1936-37 season but the usual annual catch through the mid-1940s was 400 000–500 000 t (Marr 1960). By 1952, the sardine catch had fallen disastrously and, except for a small resurgence in 1958, the sardine has "disappeared" from California waters (Fig. 2). That this collapse was unremarkable and more or less typical of

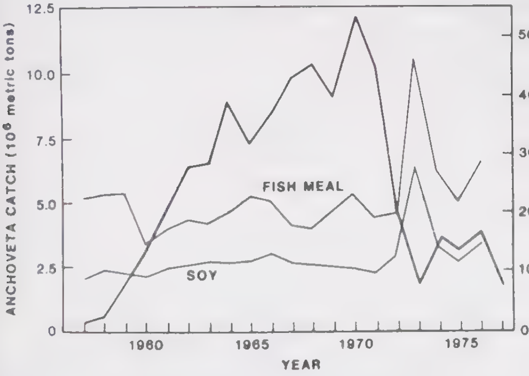

FIG. 1. The Peruvian anchoveta catch from 1957 to 1977 is shown with concomitant dollar prices for fish meal and soy on the world market (after Barber et al. 1980).

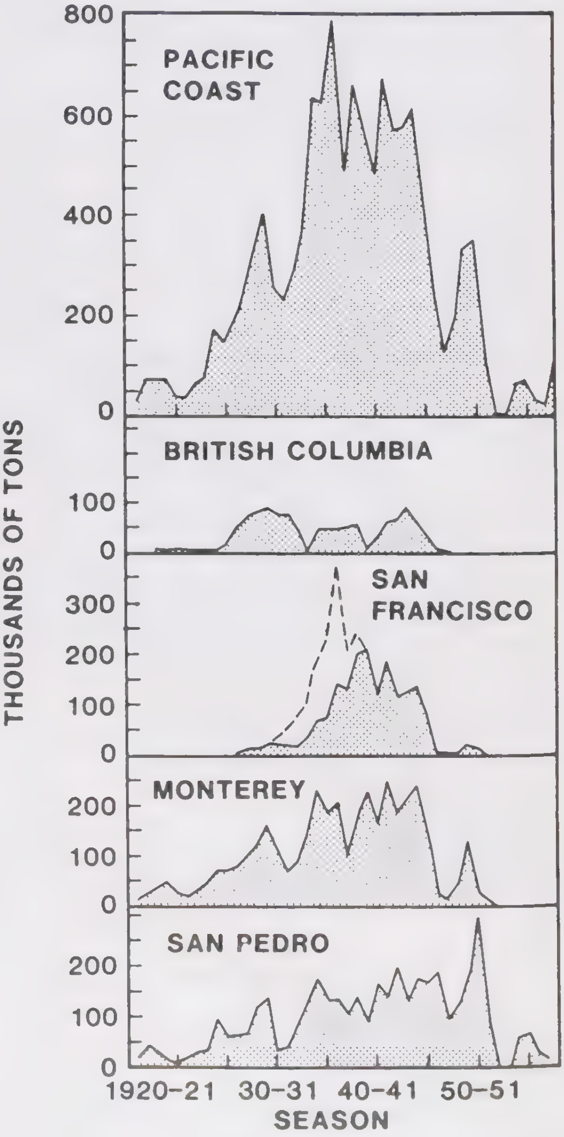

FIG. 2. North American Pacific coast sardine landings. The dashed line in the San Francisco panel indicates landings made at high seas plants (after Marr 1960).

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[1] Authorship is arranged alphabetically.

what we have come to expect from clupeoid fisheries today, can be seen by comparing similar catch records from other clupeoid fisheries. As one example, 1936 was also a peak year for the catch of the Japanese sardine, *Sardinops melanosticta*. Its disappearance was almost complete by 1945 with a small resurgence in 1951-53 (Fig. 3). Similarly, Hempel (1978) has shown that the North Sea herring (*Clupea harengus*) has seen, if not a disappearance of the fishery, a huge decline in catch from a high of 1 2 million t in 1965 to about 200 000 t in 1975 (Fig. 4). Other North Atlantic clupeoid fisheries have shown similar rapid declines (see Schumacher 1980), as has the pilchard (*Sardinops ocellata*) off Namibia, Africa (Troadec et al. 1980).

While collapses are common, so too are recoveries. Most notable in recent years have been the increased fisheries on the Japanese sardine, *S. melanosticta*, (Kondo 1980), and the Peruvian–Chilean sardine, *Sardinops sagax* (O. Rojas, Instituto de Fomento Pesquero, Santiago, Chile, personal communication). At its peak in 1936, the catch of the Japanese sardine was slightly over 1.6 million t. After its decline, very few sardines were caught from 1960 through 1972. Figure 3 illustrates the dramatic comeback made by this species, with the 1981-82 catch at about 2.5 million t. Kondo (1980) has said that this resurgence is attributable to the outstanding success of the 1972 year-class. Lea documented a similar outstanding year-class (1904) of herring (*Clupea harengus*) which sustained the North Sea herring fishery for many years (cited by Hardy 1959).

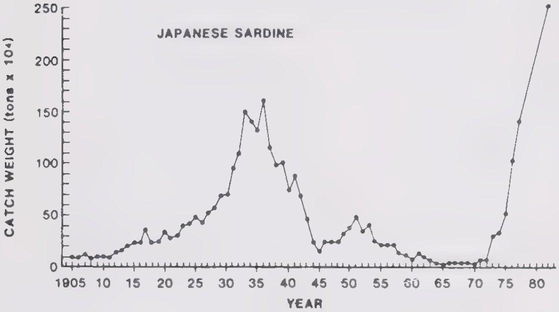

FIG. 3. Catch of the Japanese sardine (after Kondo 1980; and K. Kondo, Tokai Regional Fisheries Research Laboratory, Tokyo, Japan, personal communication).

The loss of the Peruvian (and Chilean) anchoveta fishery is being offset, albeit not completely, by an increase in the catch of the Peruvian–Chilean sardine (Fig. 5). A comparison of Fig. 1 and 5 shows that the anchoveta declined in both Peruvian and Chilean waters simultaneously, coincident with a widespread El Niño condition, an unusual warming of the anchoveta habitat. Similarly the sardine catch has increased explosively in both countries. This is not to suggest that species from other fish families do not have similar dramatic ups and downs. Haddock (*Melanogrammus aeglefinus*) for example, has shown a remarkable increase in its North Sea population during a simultaneous collapse in the herring population (Hempel 1978).

While fishing is an obvious source of mortality, scientists who have studied the fluctuation of fish populations have not yet come to any definitive conclusion as to what degree fishing is the source of any clupeoid

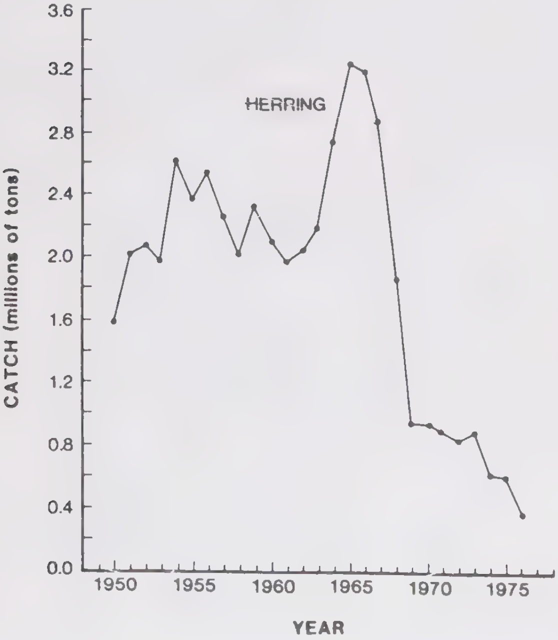

FIG. 4. Catch of the North Sea herring (after Schumacher 1980).

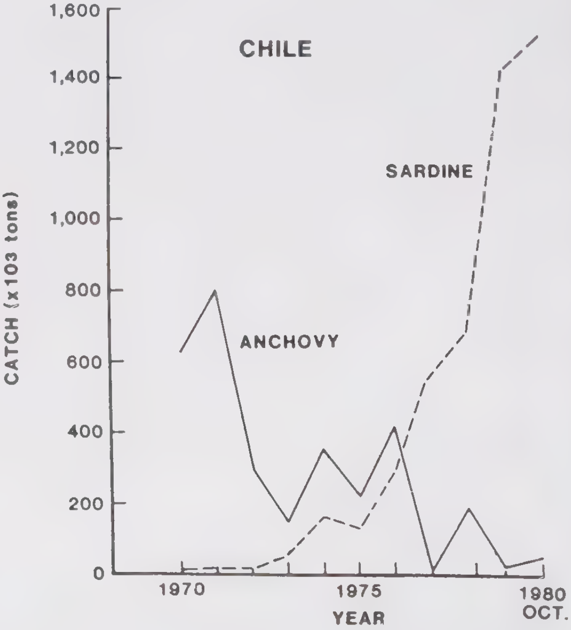

FIG. 5. The 1970–80 Chile catch of the Peruvian–Chilean anchovy and sardine (O. Rojas, Instituto de Fomento Pesquero, Santiago, Chile, personal communication).

collapse. In an interesting paper, Clark and Marr (1955) argued for opposing viewpoints regarding the loss of the Pacific sardine. Clark believed that each Pacific sardine year-class was related to stock size and was density dependent. Marr, on the other hand, argued that poor year-classes were due to adverse environmental factors (chiefly temperature affecting spawning time) and caused the sardine's disappearance (density independence); however, he added that at the smallest stock sizes year-class size is a function of spawning stock size. Logically, some form of density independence must be operative to account for fish population outbursts, but neither Clark nor Marr commented on what might induce a successful year-class at low stock levels.

In an elegant paleoecological investigation, Soutar and Isaacs (1969, 1974) sought to reconstruct a history of the fluctuations in some of the common fish populations off California by identification of fish scales in undisturbed sedimentary cores from local anaerobic basins, such as the Santa Barbara Basin near Los Angeles. Figures 6 and 7 show nearly 2000 yr of apparent biomass fluctuations for Pacific sardine and northern anchovy (*Engraulis mordax*). Figure 8 shows that extreme biomass fluctuations, both precipitous declines and rapid increases, are common where no fisheries have ever been present.

A few years after the Pacific sardine collapse, the northern anchovy *Engraulis mordax* began to increase in California and Baja California waters. By 1960, the sardine was virtually gone, but egg and larval surveys indicated that the anchovy had become the abundant clupeoid in California waters. By 1965, the anchovy spawning biomass exceeded 4.5 million t. Except for a brief period in the early 1950s, there was no substantial fishery for this species until 1966. A substantial decline in the population occurred between 1975 and 1978. Although a small fishery (ca. 200 000 t) was established during those years, only a tiny fraction of the decline from 3.5 million t to 1 million t could be accounted for by fishing. Studies over the past decade on the northern anchovy off California and Baja California have allowed the development of some generalizations which may be applicable to the fluctuation of clupeoid populations in general.

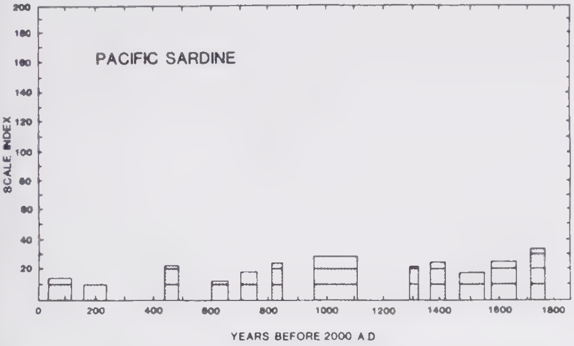

FIG. 6. Soutar and Isaacs' (1969) population indexes for Pacific sardine derived from the number of scales found in anaerobic sediments from the Santa Barbara Basin (modified after Soutar and Isaacs 1969).

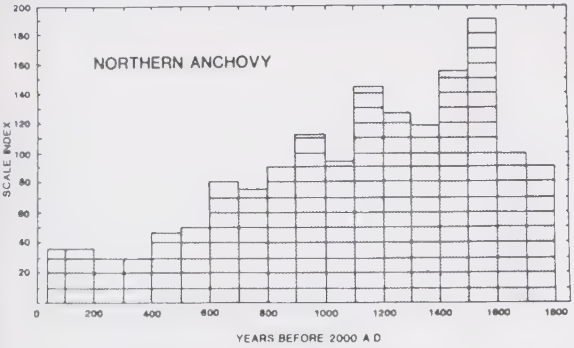

FIG. 7. Population index for northern anchovy derived from numbers of scales found in anaerobic sediments from the Santa Barbara Basin (modified after Soutar and Isaacs 1969).

Ecological Requirements for Larval Survival

Hjort's (1913) original suggestion pinpointing the early first-feeding larva as the most vulnerable stage in the life history of fishes is still the basis for many interesting hypotheses. He believed that the presence or lack of food at larval first-feeding decided the size of the year-class in annually spawning herring. This idea has been resurrected from time to time in the literature, and has received experimental support from a number of investigations where the laboratory food requirements of fish larvae have been compared with available food under natural conditions. For example, laboratory work on anchovy larvae in California (O'Connell and Raymond 1970) indicated that first-feeding anchovy larvae require higher food densities (as determined in the laboratory) than has been usually reported from its habitat (Beers and Stewart 1967); (see review by Hunter 1977).

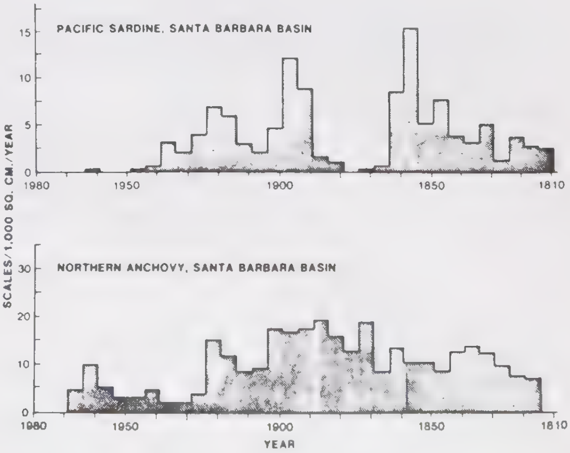

FIG. 8. Recent scale deposition rates for the Pacific sardine and the northern anchovy.

In a series of papers, Lasker (1975, 1978, 1981a) showed that food is indeed present at high enough concentrations, usually in coastal waters, at local densities sufficient to insure feeding in a high proportion of first-feeding anchovy larvae. Furthermore, he indicated that survival may be a function of ocean stability (Lasker 1981b) where maintenance of high numbers of food organisms is dependent on the lack of water turbulence. When turbulence is strong, due to storms, upwelling, etc., concentrations of food organisms may be dispersed reducing the number of food particles to below feeding-threshold densities, and making it impossible for newly feeding anchovy larvae to survive. The kind of food available is another factor, since some foods would not support growth in anchovy larvae.

Egg Mortality and Larval Production

Mortality of northern anchovy eggs has only recently received much attention in relation to subsequent larval survival. Hunter and Kimbrell (1980) determined that anchovy adults, because of their filter-feeding capability, can and do strain out and ingest congregated as well as isolated anchovy eggs. The patchiness of eggs (prey) and the schooling behavior of the adults (predators) make the coincidence of predator and prey particularly important in determining the number of eggs that will survive. Probably other schooling organisms, e.g. sardines and euphausiid shrimps, (Theilacker and Lasker 1974) can reduce the number of surviving offspring.

In 1980 and 1981, very similar overall egg production rates occurred, but egg mortality rates were very different in the two successive years (Table 1). This resulted in a very much higher number of early larvae in 1981 than in 1980. At this writing (July 1982), the 1981 year-class seems to be a very poor one. Thus, environmental factors having little to do with the number of larvae produced seem the more likely explanation for the resultant year-class size in this case.

Recent studies by Methot (1981) incorporating birth date determination of anchovy recruits in which he used a precise aging technique, otolith daily annulus counts (Brothers et al. 1976; Methot and Kramer 1979), permit the determination of relative survival through the spawning and larval production period. Northern anchovy have a protracted spawning period from December through May. Peak spawning, however, is confined to the February–March–April period. By age-dating recruits resulting from the 1978 and 1979 spawning period, a relative picture of larval survival was obtained and comparisons could be made with the abiotic factors prevailing during the larval period. Methot (1981) showed that in 1978, despite the heaviest larval production in late February, the majority of recruits were born in March and April (Fig. 9). Lasker (1981a) attributed this to the series of severe storms that swept through the anchovy spawning grounds in December 1977 through February 1978 and ceased only by mid-March 1978. Turbulence from these storms appeared to reduce larval food concentrations below threshold for first-feeding and should have resulted in reduced larval survival. However, data from 1979 showed a reversed pattern with higher survival in winter relative to spring (Fig. 9). Methot (1981) favors the idea of Parrish et al. (1981) that spring upwelling may result in transport of larvae offshore where they are lost to the main population.

Correlations between menhaden year-class strength and Ekman transport characterize the interesting work of Nelson et al. (1976). Because of the estuarine dependence of menhaden larvae, these must be carried into estuaries from offshore spawning grounds in order to survive. Nelson et al. (1976) showed that indexes of westward transport toward U.S. east coast estuaries from offshore spawning areas were positively correlated with indexes of yearly survival.

Larval drift has also been implicated in excessive larval mortality of other species, for example by Parrish and MacCall (1978) who studied Pacific mackerel (*Scomber japonicus*) year-class survival in relation to upwelling indexes. They found strong negative correlations between upwelling and good year-classes. The Kondo (1980), Nelson et al. (1976), Methot (1981), Parrish et al. (1981), and Lasker (1981a) conclusions, while arrived at by different approaches, all depend on Hjort's (1913) idea that it is lack of food that affects larval survival and assumes the effect of predation on eggs and larvae to be minimal or constant.

TABLE 1. Variability of standing crop of larvae due to differential mortality.

Year	Specific egg production $\left(\frac{\text{eggs}}{\text{g} \cdot \text{d}}\right)$	Survival to hatch	Exponential mortality rate for larvae (d^{-1})	Calculated specific standing crop of larvae $\left(\frac{\text{larvae}}{\text{g} \cdot \text{d}}\right)$	Larval abundance from surveys (10^{12} larvae)
1980	30.65	0.359	0.168	65.5	18.11
1981	32.60	0.705	0.164	140.1	28.60

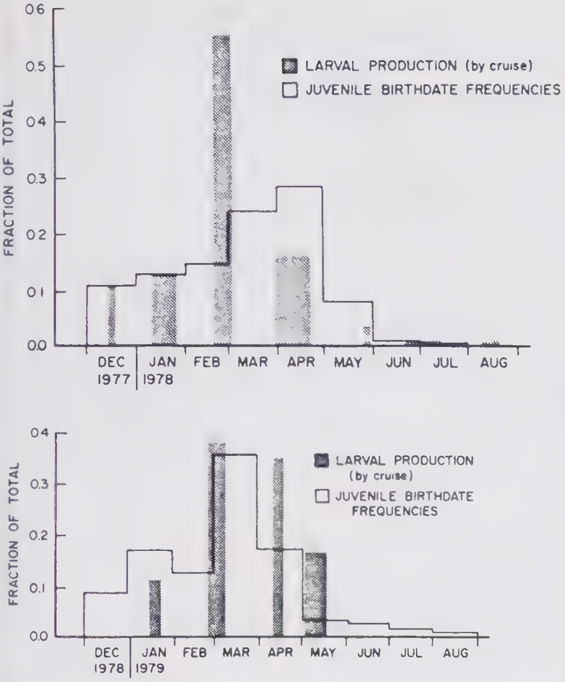

FIG. 9. Birthdate frequencies of juvenile anchovies compared to the larval production. Hatched bars indicate each of seven cruises (after Methot 1981). Top, December 1977–August 1978; Bottom, December 1978–August 1979.

Differential Fecundity

Compounding this complexity is the differential fecundity of the northern anchovy from year to year. For as yet unknown reasons, the northern anchovy increased its egg production per gram of female per day by 30% in 1981 over 1980. Thus the interplay of a variety of factors must determine eventual recruitment; (1) female fecundity and egg production; (2) egg mortality which depends on the number and coincidence of egg predators including the spawners themselves; (3) larval food availability and physical ocean factors including turbulence and drift; and (4) larval mortality (including starvation and predation). To what degree each of these contributes to larval survival is as yet unknown.

Cannibalism and Stock Expansion

Fishery management usually relies on conventional "black box" models of overall population dynamics such as production models or stock–recruitment relationships (SRR). These models are assumed to represent an integration of local mechanisms over the extent of the stock in space or time. Rarely are specific mechanisms identified and integration actually performed. However, when this is attempted, the results may differ from conventional models.

Behaviorally, anchovy spawning appears to be a risk-spreading strategy of covering all possibilities. Individual anchovies may spawn at 6- to 7-d intervals, or about 20 times in a season (Hunter and Leong 1981), so that an individual's eggs encounter a wide temporal range of environmental conditions. Within the geographic limits of spawning, eggs occur ubiquitously.[2] As a result of this widespread temporal and geographic coverage, conditions favorable for larval survival, although relatively unpredictable, tend to be utilized wherever and whenever they occur.

Murphy (1977) observed that clupeoid fishes characteristically expand and contract their range with changes in overall stock abundance. This behavior is demonstrated clearly by the distribution and abundance of anchovy larvae off southern California (Fig. 10). MacCall (1980a) has shown that this geographic behavior is a logical consequence of density-dependent habitat selection, given the following assumptions: (1) the spawning habitat is most favorable near the center of the range, and deteriorates toward the periphery; (2) the local spawning habitat becomes less favorable as local density of spawners increases, for example, because of cannibalism (e.g. Hunter and Kimbrell 1980); and (3) fish individually attempt to spawn in the most favorable locations. The resulting distribution of spawner abundance should approach the "ideal free distribution" of Fretwell and Lucas (1970) wherein all fish experience approximately the same quality of spawning habitat. At low stock abundances the fish are concentrated in the most favorable localities. At high abundances the density increases in those previously favorable areas, but due to a density-dependent decrease in the quality of those habitats, the stock also expands into surrounding previously unoccupied areas of marginal quality. Thus, in terms of the risk spreading spawning strategy, the expected reproductive success in formerly poor peripheral areas now is equally attractive to the expected reproductive success in central preferred areas that have a high risk of cannibalism. While fish are probably unable to sense these risks directly, information such as water temperature and food abundance (which responds to grazing intensity) may be sufficient to govern adaptive geographic movements.

The overall effect is expansion of the range as stock abundance increases. Local density (and consequently, density-dependent effects) increases more slowly than does total abundance. If fishermen concentrate their activity in areas of highest density, catch per unit effort (C/f) will be insensitive to changes in total abundance even if C/f accurately reflects true local density. MacCall (1976) suggested that Pacific sardine C/f varied as a power function of stock abundance (N), $C/f = aN^b$, where $-1 < b < 0$, as is consistent with the above geographic behavior.

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[2] While the widespread extent of anchovy spawning has long been recognized, the degree of spatial and temporal saturation is remarkable. In recent California Current ichthyoplankton surveys using a small net (0.05 m^2 opening), three nightly age groups of anchovy eggs are discernible from embryonic development prior to hatching. Of those samples containing at least three eggs of any age, about 50% contained eggs from all three previous nights of spawning.

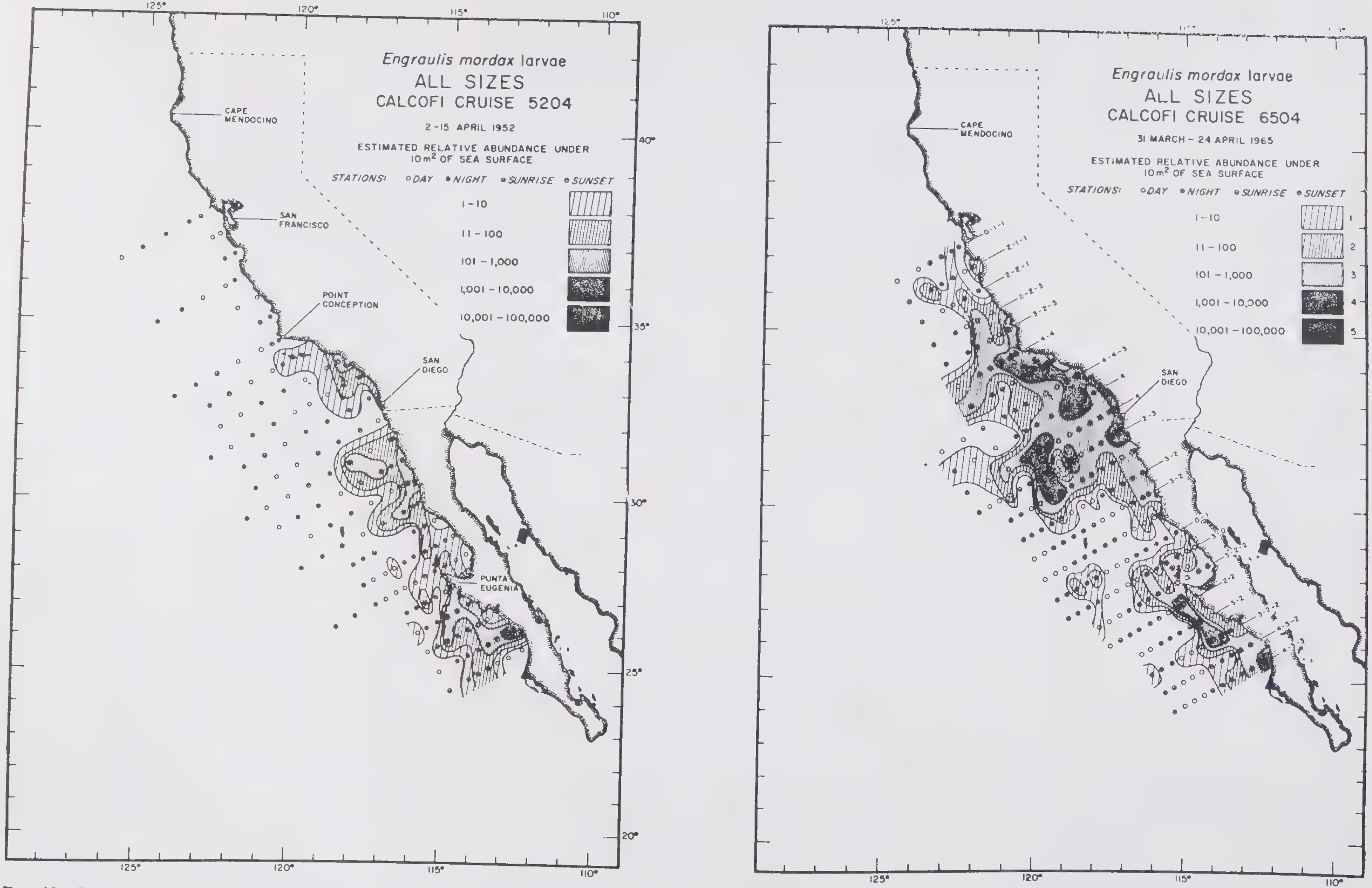

FIG. 10. Geographic distribution of northern anchovy larvae at low and high population sizes.

This geographic expansion model produces some surprising departures from the traditional fishery models. Gulland (1977) reports a production model originally developed by W. W. Fox Jr. wherein C/f varies according to the above power function. The resulting production model predicts stock collapse at levels of effort only slightly above that producing maximum sustainable yield (MSY). Also, depleted stocks would have difficulty recovering from this collapse unless effort is reduced drastically. Csirke (1980) describes a stock–recruitment model of Ricker form, where egg production is proportional to abundance, but subsequent survival is a function of mean adult density (measured by C/f) rather than total abundance. Csirke's model is therefore consistent with the above geographic expansion model. While local dynamics show decreasing recruitment at high density, geographic expansion offsets this local decrease, so that the overall stock–recruitment relationship (SRR) loses much of the domed shape characteristic of the traditional Ricker model. The resulting SRR appears almost asymptotic (Fig. 11).

The shape of the general clupeoid SRR has been open to debate. Harris (1975) distinguished between stock-dependent (intercohort) processes, which tend to produce a domed SRR, and density-dependent (intracohort) processes, such as competition among larvae, which tend to produce a less curved, asymptotic SRR. Cannibalism has often been suggested as the most likely regulatory mechanism for filter feeding clupeoid fishes (Murphy 1967; Csirke 1980), but as noted above, this mechanism produces a domed SRR. Cushing's (1971) empirical observations of clupeoid SRRs indicated that they are not domed, but only slightly curved. Stock and recruitment data on California sardines and anchovies are in agreement with Cushing (MacCall 1979, 1980b). According to Harris' (1975) criteria, Cushing's contention that clupeoids lack a strongly domed SRR would require that cannibalism not be a major regulatory mechanism.

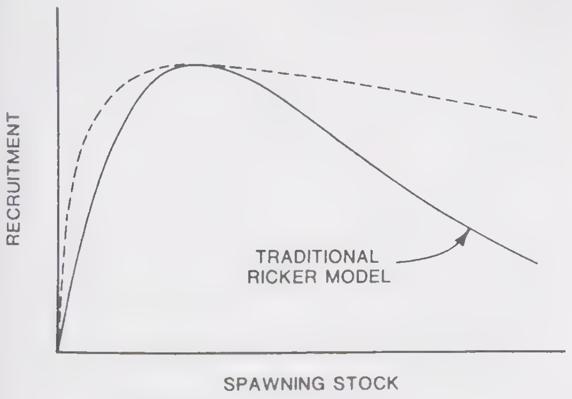

FIG. 11. Modification of the Ricker stock–recruitment relationship due to geographic expansion at increased abundance (dashed line).

Hunter and Kimbrell (1980) have compared abundances of eggs in northern anchovy stomachs with production of eggs from their gonads, and concluded that cannibalism may account for 32% of the egg mortality. An increased mortality rate of eggs at larger anchovy population sizes also can be inferred from the relationship between egg abundance and production of hatched eggs or larvae (Fig. 12). Egg abundance is calculated as a regional census estimate according to the method of Smith (1972). This abundance was divided by the mean time to hatching as indicated by the mean water temperature. Larva production is derived from the time-zero intercept of abundance upon larval age (Hewitt 1982). At large population sizes, production of larvae per egg decreases as can be seen by the deviation of the relationship from proportionality in Fig. 12. Due to the inactive nature of eggs, this differential mortality is more likely stock dependent than density dependent (sensu Harris 1975, see above).

The geographic expansion model allows reconciliation of a stock-dependent regulatory mechanism and a slightly curved SRR. If accompanied by adaptive changes in geographic distribution and utilization of habitat, a stock-dependent process such as cannibalism need not produce a strongly domed SRR. The less curved SRR which results implies weaker regulation of abundance (i.e., weaker density dependence). As a corollary, studies of clupeoid fishery productivity which wrongly assume the strongly density-dependent Ricker curve will tend to overestimate MSY, underestimate the biomass necessary to produce MSY, overestimate the fishing effort necessary to produce MSY, and generally overestimate the resilience to overfishing.

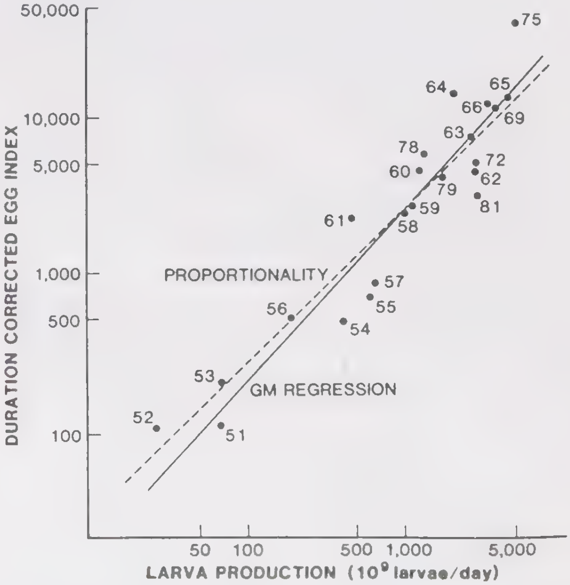

FIG. 12. Relationship between anchovy egg abundance (corrected for temperature-specific duration) and production of hatched larvae. The probability that the two variates are proportional is approximately 10%.

Reconsideration of Paleosedimentary Evidence and Sardine–Anchovy Competition

Fish scales preserved in anaerobic sediments of the Santa Barbara Basin have provided several clues to the nature of the sardine–anchovy relationship (Soutar and Isaacs 1969, 1974). Unfortunately, interpretation of these clues has been equivocal. The evidence has been of two types: scale deposition rate (SDR) is assumed to be indicative of fish abundance, while the size (width) of the scales is assumed to be indicative of fish size.

Soutar and Isaacs (1974) show scale deposition rates for thirty-one 5-yr periods (pentads) from 1810 to 1965 A.D. (Fig. 8). The most prominent feature of these time series as shown by Smith (1978) is much lower variability of the anchovy population relative to the sardine population. This has been taken to be evidence that the sardine has been the more variable of the two, but this conclusion must be tempered by our knowledge of the geographic behavior of clupeoid stocks. The Santa Barbara Basin is near the central area of preferred anchovy habitat, so we must expect local anchovy abundance to be "buffered," that is, to vary much less than relative abundance of the total central stock (cf. Fig. 10). Soutar and Isaacs' (1974) calibration of anchovy SDR (Fig. 13) confirms this tendency toward a "buffered" response to changes in central stock abundance. Thus anchovy abundance is likely to have been more variable than is suggested by the time series of its SDR in the Santa Barbara Basin. We know less about the preferred habitats of sardines in the absence of fishing, and whether the Santa Barbara Basin is central or marginal. The SDR would correspondingly reflect a buffering or exaggeration of the total stock abundance. Soutar and Isaacs' (1974) calibration to sardine biomass (Fig. 13) is imprecise, but suggests a slight tendency toward exaggeration of changes in total abundance.

Soutar and Isaacs (1974) conclude that the low sardine SDR from 1865 to 1880 is similar to those following 1940 (Fig. 8), making the latter decline indistinguishable from previous natural fluctuations. While this interpretation superficially appears justifiable, we must note that sardine abundance has not recovered in the past 40 yr, contrary to the pattern of the 1870s. Soutar and Isaacs' (1974) calibration of sardine SDR loses definition at about 700 000 t biomass, where zero counts become common (Fig. 13). Thus the sardine biomass could have ranged from 0.5 to 1 million t during the "disappearance" in the 1870s. In contrast, recent sardine abundance has been less than 10 000 t (MacCall 1979). In view of this supplementary information, the scale deposition data do not support the previous conclusion that the recent decline in sardine abundance is indistinguishable from natural prefishery fluctuations. Also, sardines took 15 yr or less to recover from the relatively low abundance of the 1870s. It is reasonable to expect a similar capacity for recovery nowadays off California, if sufficient reserve biomass were to be maintained by an appropriate program of fishing restraint.

In an attempt to define the nature of sardine–anchovy interactions, Soutar and Isaacs (1974) calculated a Spearman rank correlation coefficient of +0.34 between sardine and anchovy SDR. The negative correlation that would be expected from the commonly assumed competition between these species is not evident at the 5-yr or longer time scale. Rather, there appears to be a slight tendency toward parallel variation, perhaps due to similar responses to large-scale environmental conditions. This allows a speculation that the increase in anchovy biomass from 1950 to 1975 could well have been accompanied by an increase in sardine biomass, had there not been an intense fishery on the latter. Therefore we invoke a density-dependent explanation for potential long-term recovery, although random, density-independent effects dominate over the short term.

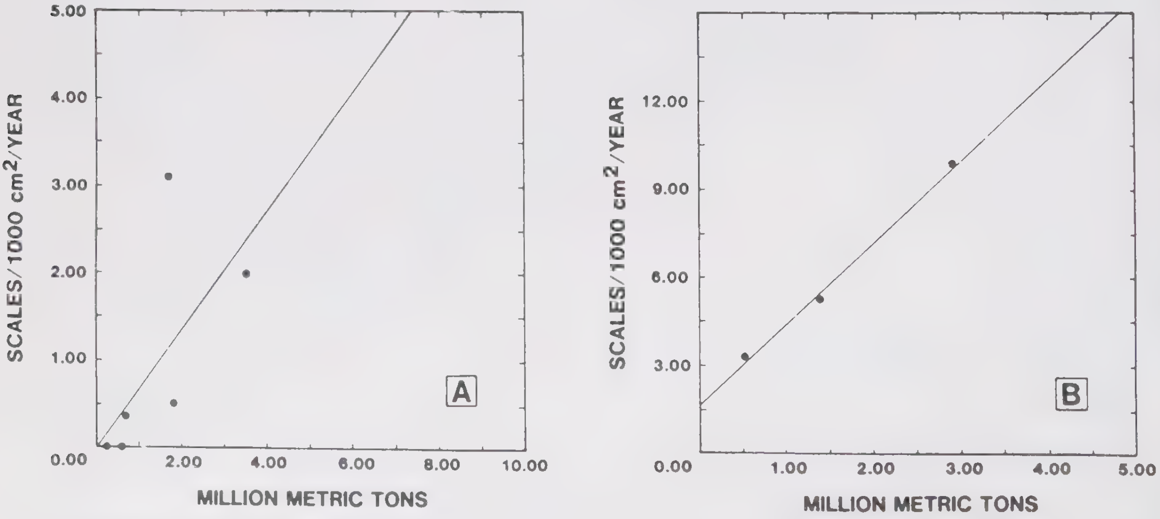

FIG. 13. Relationship of fish scale deposition rate to stock abundance off California. A. sardine, B. anchovy (adapted from Soutar and Isaccs 1974).

The evidence from scale sizes is more suggestive of possible sardine–anchovy interactions. Previous attempts to infer individual fish lengths from scale widths have been confounded by the range of scale sizes on individual fishes. However, we can more safely infer relative changes in the distribution of fish lengths from relative changes in the distribution of scale widths, under the usual assumption that scales grow in proportion to fish length. The 31 pentads from 1810 to 1965 contained 326 anchovy scales for which widths could be determined (data provided by A. Soutar). If these scales are separated into two groups corresponding to high and low anchovy SDR (respective weighted mean SDRs are 16.9 and 9.7 scales/1000 cm^2/yr), the two scale width distributions are nearly identical. However, if the scales are separated into groups corresponding to high and low sardine SDR (respective weighted mean sardine SDRs are 7.0 and 1.2 scales/1000 cm^2/yr, weighted mean anchovy SDRs are both 13.3 scales/1000 cm^2/yr), the width distributions are significantly different (Fig. 14, Kolmogorov–Smirnov D Statistic: $P < 0.01$). The mean anchovy scale width during periods of high sardine SDR is 4.94 mm, while during periods of low sardine SDR, the mean width is 5.71 mm. Assuming a cubic relationship between mean scale width and mean fish weight, the average anchovy is approximately 54% heavier during periods of low sardine SDR.

While this size–abundance relationship is consistent with the competition hypothesis, it is not the only explanation. It is possible that environmental conditions favorable to sardine abundance are associated with low growth rate, higher mortality rate, or a relatively more offshore distribution of small anchovies. Anchovies have exhibited some of these phenomena since the late 1970s in southern California, where they have tended to be smaller, younger, and now mature at a relatively small size (Mais 1981; Hunter and Macewicz 1980). Coincidentally, sardines are showing signs of increased abundance (R. Klingbeil, California Department of Fish and Game, Long Beach, CA, personal communication), but are still much too scarce to have a significant impact on anchovies. These phenomena, whose causal relationships are unclear, are consistent with the paleosedimentary patterns. Unfortunately, the paleosedimentary record provides little evidence on causal mechanisms driving the patterns of apparent fish abundance.

Appreciation

Clupeoid fisheries have been studied intensely for nearly half a century. While some of the ideas presented in this paper may be new, others have existed in various forms for many years. Nonetheless, we feel that clupeoid fishery biology is approaching a new synthesis which will allow better understanding of stock fluctuations. Yet even this synthesis is not completely new: almost all the components appear in Sette's (1943) conceptual outline of the relationships among fish life history stages, fisheries, and the biotic and abiotic features of their environment (Fig. 15). Sette's paper has been a foundation of much of the subsequent research on clupeoid fisheries of California. The success of that research must be attributed, in part, to the completeness of Sette's original vision.

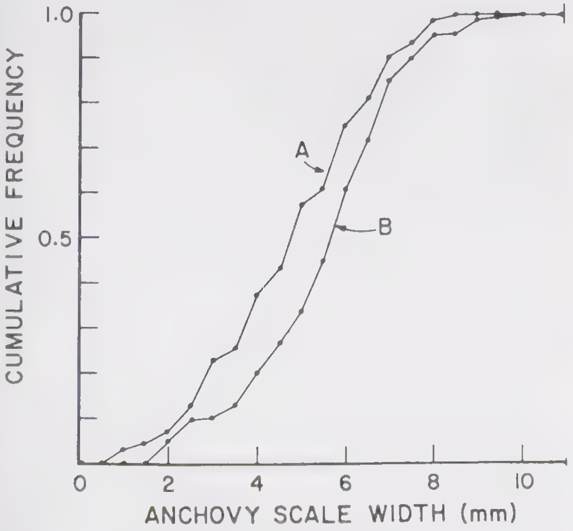

FIG. 14. Cumulative frequency distributions of anchovy scale widths from anaerobic sediments of the Santa Barbara Basin. A. Periods of high sardine scale deposition rate. B. Periods of low sardine scale deposition rate.

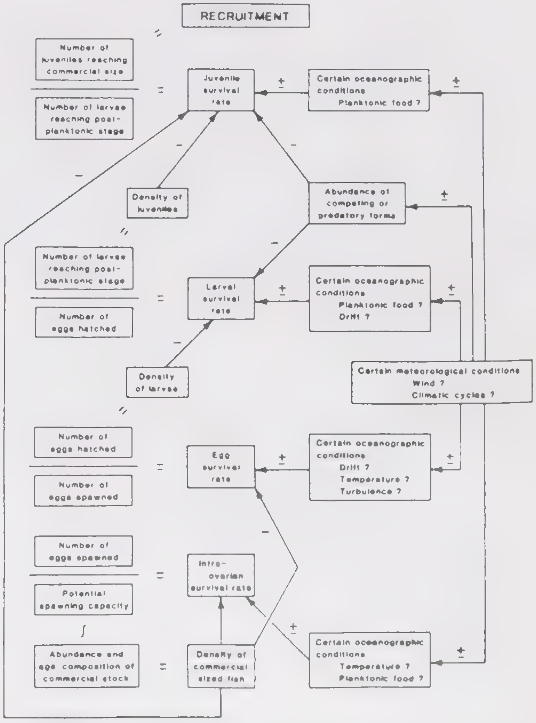
RECRUITMENT
Number of juveniles reaching commercial size
Number of larvae reaching post-planktonic stage
Juvenile survival rate
Certain oceanographic conditions Planktonic food ?
Density of juveniles
Abundance of competing or predatory forms
Number of larvae reaching post-planktonic stage
Number of eggs hatched
Larval survival rate
Certain oceanographic conditions Planktonic food ? Drift ?
Density of larvae
Certain meteorological conditions Wind ? Climatic cycles ?
Number of eggs hatched
Number of eggs spawned
Egg survival rate
Certain oceanographic conditions Drift ? Temperature ? Turbulence ?
Number of eggs spawned
Potential spawning capacity
Intra-ovarian survival rate
Abundance and age composition of commercial stock
Density of commercial sized fish
Certain oceanographic conditions Temperature ? Planktonic food ?

FIG. 15. Sette's (1943) research plan for studying recruitment of the Pacific sardine.

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THE NORTH PACIFIC ALBACORE—AN IMPORTANT VISITOR TO CALIFORNIA CURRENT WATERS

R. MICHAEL LAURS
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038

ABSTRACT

The North Pacific albacore, *Thunnus alalunga,* is a highly migratory species, valuable to domestic and foreign fisheries. Albacore are found off the west coast of North America from about central Baja California to British Columbia, Canada, from late spring through fall. U.S. fishermen traditionally harvested the resource with surface gear within a few hundred miles of the shore until the mid-1970s, when an increasing number of West Coast- and Hawaiian-based jig vessels began operating from slightly west of the date line eastward across the North Pacific. A U.S. longline subsurface fishery also appears to be developing during winter beyond 1200 miles off southern California. The albacore is also highly sought after along the U.S. west coast by a large number of sportfishermen.

At the present time none of the North Pacific albacore fisheries is under management. Statistics and analysis currently available indicate that the resource is healthy. Recent estimates of MSY range from about 92,000 MT to 166,000 MT. Since the early 1960s, total catches for all fisheries harvesting albacore in the North Pacific have fluctuated; during the past decade they have ranged from about 70,000 MT to 124,000 MT.

Results from recent tagging studies suggest (1) that there are at least two substocks of fish constituting the North Pacific albacore population and (2) that these substocks have different migratory patterns. Off North America the separation in the proposed substocks occurs at Cape Mendocino, California, near 40°N. The proposed northern substock of fish makes trans-Pacific migrations between the eastern and western North Pacific, resulting in an exchange of fish between the northern area of the U.S. fishery and the Japanese livebait and gill net fisheries, and the longline fishery west of 180°. The proposed southern group of fish appear to enter the U.S. fishery south of about 40°N and are also fished by the longline fisheries east of 180°.

The migration, distribution, availability, and vulnerability of albacore are markedly influenced by oceanographic conditions in the North Pacific, notably by oceanic fronts. Recent research using acoustic telemetry methods to determine the location and swimming depth of free-swimming albacore, in conjunction with oceanographic observations made by ship and satellite suggests that water clarity's effect on the tuna's ability to see its prey is an important mechanism underlying the aggregation of tuna in the vicinity of oceanic fronts.

RESUMEN

Thunnus alalunga, albacora del Pacífico Norte, es una especie que efectúa amplias migraciones, manteniendo pesquerías nacionales y extranjeras de elevado valor económico. *T. alalunga* se encuentra desde finales de primavera hasta finales del otoño en aguas de las costas occidentales de Norte América, aproximadamente desde la parte central de Baja California (México) hasta la Columbia Británica (Canadá). Los pescadores de los Estados Unidos utilizan artes que operan en aguas de superficie, abarcando una zona que se extiende varios cientos de millas mar afuera; pero desde mediados de la década de 1970-1980, aumentaron los barcos al curricán en la costa del oeste y los de base en Hawaii, y así esta pesquería va avanzando en el Pacífico progresivamente hacia el este desde los 180° de longitud. Los Estados Unidos pescan con palangre durante el invierno, abarcando aguas más profundas, extendiéndose a más de 1200 millas del Sur de California. El albacora es también muy apreciado en la pesca deportiva, que opera a lo largo de las costas occidentales de los Estados Unidos.

Hasta ahora ninguna de las pesquerías de albacora ha sido sometida a regulaciones. Las estadísticas y análisis de los datos parecen indicar que esta pesquería logra mantenerse en buenas condiciones. Estimaciones recientes indican que las reservas de estas poblaciones alcanzan de las 92,000 a las 166,000 Toneladas métricas. Desde principios de la década de 1960-1970, las capturas totales, incluyendo todas las pesquerías de albacora en el Pacífico septentrional, han fluctuado oscilando durante la década pasada entre 70,000 hasta 124,000 Toneladas métricas.

Los resultados obtenidos mediante marcado de peces sugieren que en el Pacífico Norte hay dos poblaciones de albacora, las cuales presentan distintas rutas migratorias. La separación de estas propuestas pobla-

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ciones en la zona de América del Norte, se presenta en las inmediaciones de Cabo Mendocino, California, aproximadamente a los 40°N. Los peces de la propuesta población nórdica efectuan migraciones transoceánicas entre el Pacífico oriental y occidental, resultando así un intercambio de peces entre la pesquería del norte de los Estados Unidos y las pesquerías japonesas con cebo vivo y trasmallos y la pesquería con palangre al oeste de 180°. El propuesto grupo meridional de peces entran al parecer la pesquería de los Estados Unidos al sur de los 40°N, y también se pescan con palangre al este de los 180°.

La migración, distribución, presencia y vulnerabilidad del albacora se ven influidas notablemente por las condiciones oceanográficas del Pacífico Norte, principalmente por los frentes oceánicos. Investigaciones recientes utilizando métodos telemétricos acústicos para determinar la distribución y localización en profundidad del albacora, en conjunción con observaciones oceanográficas efectuadas desde barcos y satélites, revelan que el comportamiento de agrupación de estos peces en las inmediaciones de los frentes oceánicos está condicionada más por el alimento que por los mecanismos termo-fisiológicos.

INTRODUCTION

Albacore tuna, *Thunnus alalunga* (Bonneterre), is a highly migratory tuna that supports important U.S. commercial and recreational fisheries and several foreign fisheries in the North Pacific. Over the past decade fisheries operating on North Pacific albacore have expanded, and research has yielded new information about this valuable resource. The purpose of this paper is to give an overview of the catch, effort, and catch-per-unit-effort trends of fisheries harvesting the North Pacific albacore and to provide information on the condition of the stock. Also, results from selected research investigations dealing with albacore oceanography and biology will be given.

FISHERIES HARVESTING NORTH PACIFIC ALBACORE

Japan and the U.S. account for the majority of the catches of North Pacific albacore—approximately 70% and 28%, respectively, from 1961 through 1978. Canada, Korea, and Taiwan each land about 0.5% to 1% of the total catch.

Historically, the Japanese have had two distinct fisheries harvesting albacore—a pole-and-line surface fishery operating during spring and summer and a longline subsurface fishery operating during winter. In 1978 a third Japanese fishery gained importance with the dramatic expansion of summer gill net fishing targeted on albacore.

For several decades the pole-and-line fishery extended eastward from near the coast of Japan to about 150°E; however, in the early 1970s it was expanded to east of the date line. The Japanese longline fishery is executed across much of the North Pacific, and by 1981 gill net operations had spread almost entirely across the North Pacific to within several hundred miles of the North American coast.

The U.S. fishery for albacore, which began in the early 1900s, uses surface trolling and pole-and-line fishing gears (Dotson 1980). The fishing takes place during summer and autumn in waters within a few hundred miles of the coast between central Baja California and British Columbia. Major geographical variations in the location of the fishing occur; during some periods it is centered in waters off the Pacific Northwest, during others, off southern-central California (Laurs et al. 1976). These geographical shifts in the location of the fishing have been linked to variations in environmental conditions (Clark et al. 1975). In 1975 the U.S. troll fleet began a broad extension of its operating range (Laurs and Nishimoto 1977). In recent years 75 to 100 vessels have started to fish near the date line about May, and to operate eastward across the mid-North Pacific to end the season in autumn off the coast of the U.S.

Recently, the U.S. albacore industry conducted a series of exploratory fishing operations to evaluate the feasibility of a winter U.S. longline fishery for albacore in the eastern Pacific (Laurs et al. 1981). The results of the experiments are encouraging, and a number of vessels have indicated a desire to participate in this new albacore fishery for the U.S.

CATCH, EFFORT, AND CATCH-PER-UNIT-EFFORT TRENDS

Catch Trends

Estimated annual catches of North Pacific albacore by country and gear type are given in Figure 1 for years 1961-79 (Bartoo and Kume 1982a) and in Table 1 for years 1962-81 (Bartoo and Kume 1982b). Since the early 1960s, total catches of North Pacific albacore fluctuated annually, but showed an increasing trend until 1976, when a peak of nearly 124,000 MT was recorded. During the early and middle 1970s, the increased catches reflected a rapid development of the Japanese pole-and-line fishery. In 1977, the catch declined by 40% compared to the average of the preceding 6 years; the decline was due primarily to the sharply reduced Japanese pole-and-line catch. Catches in 1978 recovered to the 1974-77 average of 97,000 MT, but in 1979 the catch again declined, mainly because the U.S. catch fell to its lowest point in nearly 40

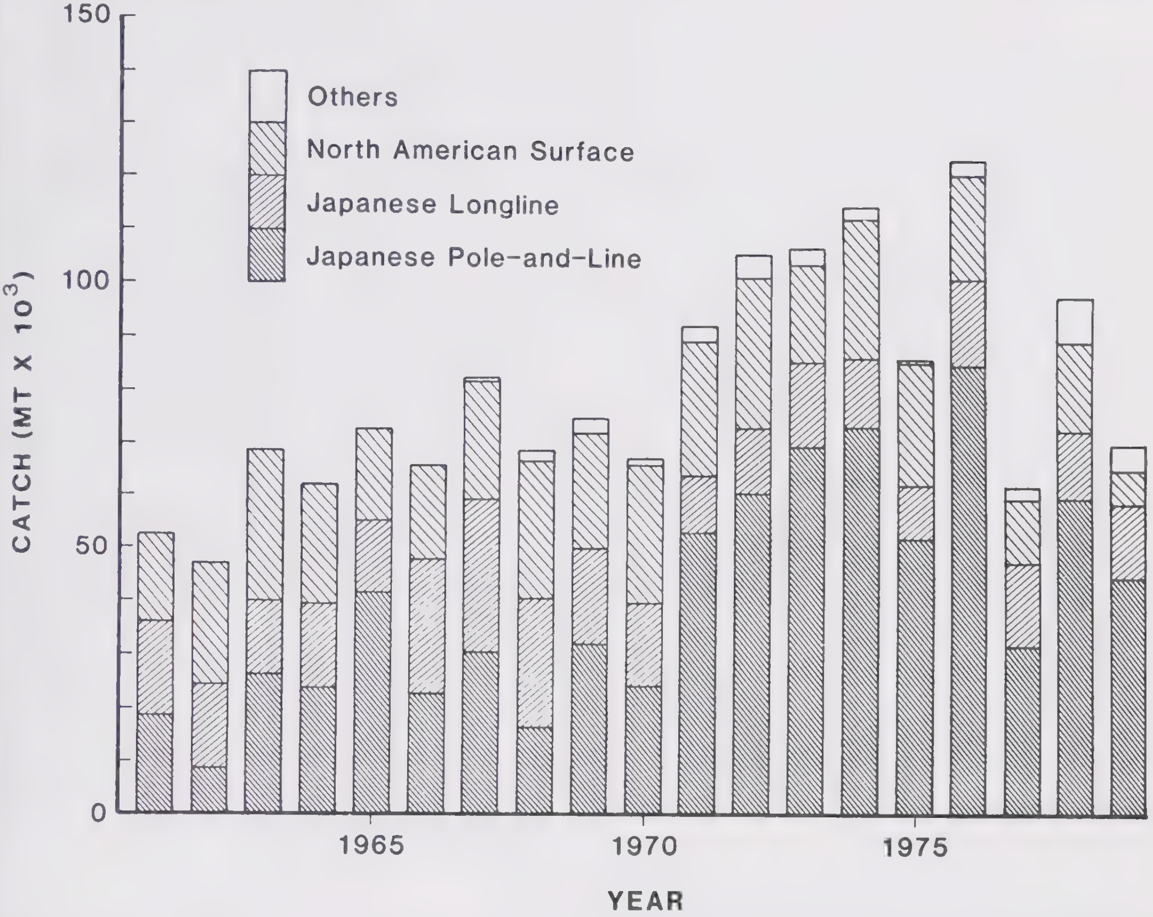

Figure 1. Annual catches of North Pacific albacore in the Japanese pole-and-line, Japanese longline, and North American surface fisheries, 1961-79 (Bartoo and Kume 1982a).

years—a little more than 7,000 MT. In 1980, the total catch increased to over 74,000 MT. It appears that the 1981 total catch was about 76,000 MT. The 1981 Japanese pole-and-line catch of albacore declined to about 26,000 MT, its lowest level since 1970, but this was offset by a dramatic increase in the Japanese drift gill net catch to nearly 20,000 MT.

Effort Trends

Effort trends within the U.S. troll fishery and the Japanese pole-and-line and longline fisheries are shown in Table 2 (Bartoo and Kume 1982b). The U.S. troll effort has remained rather stable except for 1972 and 1979 when the amounts of effort exerted were high and low, respectively. Effort by the Japanese longline fishery, the longest historical series available, shows considerable variability, but is relatively constant in the late 1970s at a level corresponding to about 75% of that in the 1960s and about 150% of that in the early 1970s. The Japanese pole-and-line effort increased substantially in the 1970s—primarily as the result of larger vessels entering the fishery—to levels almost triple those of the 1960s. In recent years the number of vessels in the 100 to 200 gross ton class, which account for more than 80% of the Japanese pole-and-line albacore catch, has declined (Bartoo and Kume 1982b). However, the number of large (greater than 100 gross tons) drift gill net vessels has been increasing, and the gill net fishery has expanded its operations farther eastward, with some fishing as far east as 135°W[1].

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[1] Bartoo, N. 1982. United States albacore surface fishery catch distribution determined from log book records. Seventh North Pacific Albacore Workshop. Working Paper NPALB/82/12. 26 p.

TABLE 1
Catches for North Pacific Albacore in Metric Tons, 1952-81

	Japan					Taiwan & Korea	United States				Canada	
Year	Pole-and-line	Long-line	Gill net	Other gear	Total	Longline	Baitboat	Jigboat	Sport	Total	Jigboat	Grand Total
1952	41,386	26,687		237	68,710			23,843	1,373	25,216	71	93,997
1953	32,921	27,777		132	60,830			15,740	171	15,911	5	76,746
1954	28,069	20,958		38	49,065			12,246	147	12,393	—	61,458
1955	24,236	16,277		136	40,649			13,264	577	13,841	—	54,490
1956	42,810	14,341		57	57,208			18,751	482	19,233	17	76,458
1957	49,500	21,053		151	70,704			21,165	304	21,469	8	92,181
1958	22,175	18,452		124	40,731			14,855	48	14,903	74	55,708
1959	14,252	15,502		67	30,121			20,990	—	20,990	212	51,323
1960	23,156	17,369		76	42,601			20,100	557	20,657	5	63,263
1961	18,636	17,437		268	36,341		2,837	12,054	1,355	16,246	4	52,591
1962	8,729	15,764		191	24,684		1,085	19,753	1,681	22,519	1	47,204
1963	26,420	13,464		218	40,102		2,432	25,142	1,161	28,735	5	68,812
1964	23,858	15,458		319	39,635	26	3,411	18,389	824	22,624	3	62,283
1965	41,491	13,701		121	55,313	16	417	16,461	731	17,609	15	72,953
1966	22,830	25,050		585	48,465	16	1,600	15,169	588	17,357	44	65,882
1967	30,481	28,869		520	59,870	17	4,113	17,814	707	22,634	161	82,682
1968	16,597	23,961		1,109	41,667	15	4,906	20,441	951	26,298	1,028	69,008
1969	32,107	18,006		1,480	51,593	21	2,996	18,826	358	22,180	1,365	75,157
1970	24,376	15,372		956	40,704	23	4,416	21,039	822	26,277	354	67,358
1971	53,198	11,035		1,262	65,495	24	2,071	22,496	1,175	25,442	1,587	92,548
1972	60,762	12,649	1	921	74,333	25	3,750	23,600	637	27,987	3,558	105,903
1973	69,811	16,059	39	1,883	87,792	35	2,236	15,652	88	17,976	1,270	107,073
1974	73,576	13,053	224	1,065	87,918	40	4,777	20,177	739	25,693	1,207	114,858
1975	52,157	10,060	166	402	62,785	28	3,243	18,926	1,243	23,412	101	86,326
1976	85,336	15,896	1,070	1,394	103,696	37	2,700	16,314	766	19,780	252	123,765
1977	31,934	15,737	688	1,039	49,398	561	1,497	10,012	619	12,128	53	62,140
1978	59,877	13,061	4,029	3,209	80.176	53	950	15,700	871	17,512	23	97,773
1979	44,662	14,249	2,856	1,280	63,047	81	303	6,253	75	6,631	289	70,050
1980	46,743	14,660	2,986	1,516	65,988	—	382	7,599	174	8,155	212	—
1981	26,000	—	20,000	—	—	—	—	—	—	15,838	200	—

Remarks:
1. Figures for 1979-81 are preliminary.
2. Japanese longline catches for 1952-60 exclude minor amounts taken by vessels under 20 gross tons. Longline catches in weight are estimated by multiplying annual number of fish caught by average weight statistics.
3. Japanese pole-and-line catches include catches by research vessels.
4. United States jigboat catches include minor amounts taken by baitboats not submitting logbooks.
5. Jigboat catches for years 1952-60 include baitboat catches.
6. United States sport catch is a minimum estimate based on partial coverage
7. Grand totals omit unknown but minor catches by longline and pole-and-line vessels of the Republic of Korea.

Catch Rate Trends (CPUE)

Nominal catch-per-unit-effort (CPUE) data for the U.S. troll fleet for 1961-70 are given in Laurs et al. (1976), and CPUE statistics for the major North Pacific albacore fisheries for 1961-81 are shown in Table 3 (Bartoo and Kume 1982b) and for 1961-79 in Figure 2 (Bartoo and Kume 1982a). CPUE within the U.S. troll fishery showed no apparent upward or downward trend from 1961-70, but declined from 1971-80. CPUEs in 1979 and 1980 were the lowest observed since records began. However, in 1981, CPUE increased to more than double the value for 1980. The catch rates over the long term have varied, being highest in the late 1960s when effort was unusually variable.

CPUE within the Japanese longline fishery showed a steady decline from the early 1950s through 1960, increased substantially through 1966, and then declined through 1971. Since then the trend in catch rate has been stable.

CPUE of the Japanese pole-and-line fishery showed a slight decreasing trend from 1962-80, except for relatively high values from 1970-76. A peak catch rate of 8 MT/fishing day was reported in 1974. The catch rate reached a low of about 3 MT/fishing day in 1977, then increased slightly before dropping to about 3 MT/fishing day again in 1981.

Condition of the Stock

In 1974 the Southwest Fisheries Center and the Far Seas Fisheries Research Laboratory in Shimizu, Japan, informally agreed to exchange research results

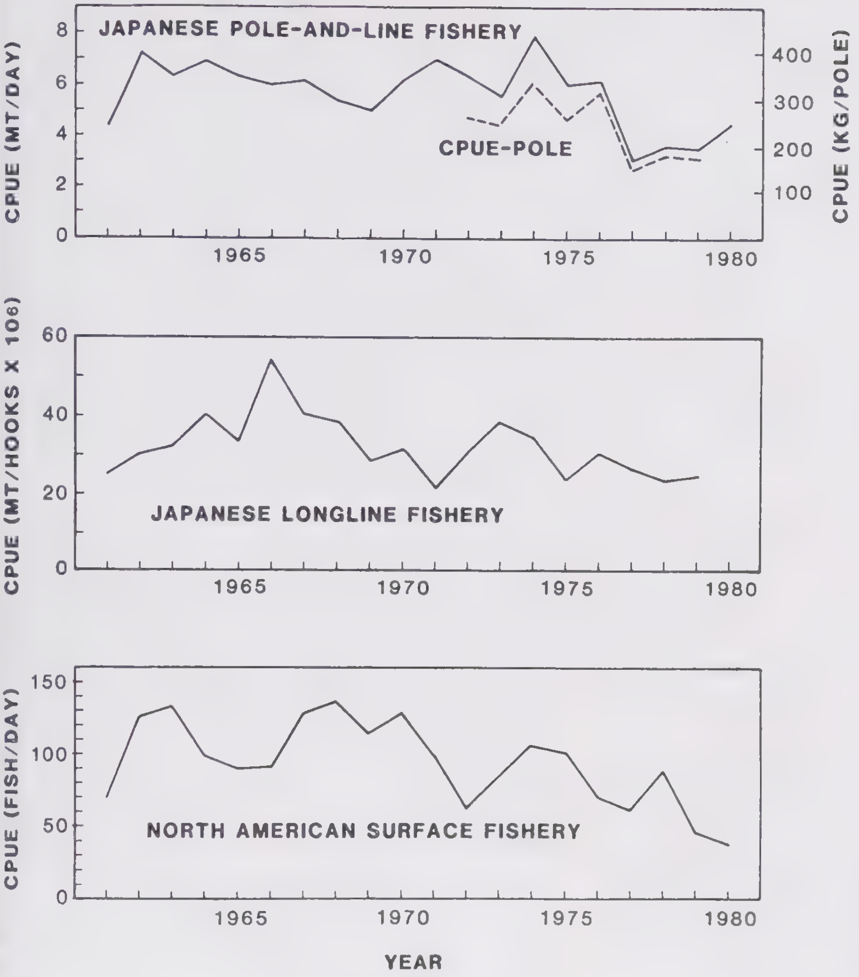

Figure 2. Annual catch rates of North Pacific albacore in the Japanese pole-and-line, Japanese longline, and North American surface fisheries, 1961-80 (Bartoo and Kume 1982a).

concerning the North Pacific albacore resource. In 1982 this agreement was extended to include the Pacific Biological Station at Nanaimo, Canada. There have been seven North Pacific Albacore Workshops held with scientists from the U.S. and Japan; in some cases scientists from Canada, Taiwan, and Korea participated. One of the objectives of the workshops is to share information for appraising the condition of the North Pacific albacore resource.

At the 1982 workshop a paper was presented on results of production model analyses based on updated abundance indices and effective effort statistics, and assuming a single stock[2]. The estimates of MSY ranged from 92,000 MT to 166,000 MT, depending largely on the assumed shape of the equilibrium yield-effort relationship. This range of estimates is consistent with results presented at past workshops. Participants at the workshop cautioned that critical assumptions underlying production model analyses may be difficult to satisfy when applied to albacore.

According to the report of the Seventh North Pacific Albacore Workshop (Bartoo and Kume 1982b),

> "Based on statistics and analyses currently available, the stock appears to be healthy. However, close monitoring is required, especially in view of increased effort in the drift gill net fishery, about which very little is known, and because of the declining catch-per-unit-effort in the major fisheries. Reliable assessment of the North Pacific albacore stocks remains a crucial task, beset by numerous problems. In particular, the measurement of effective effort is necessary, but is exceedingly difficult in the surface fisheries,

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Kume, S. 1982. An approach to evaluate the stock status of North Pacific albacore by production model analysis. Seventh North Pacific Albacore Workshop. Working Paper NPAL/82/11. 6 p.

TABLE 2
Estimated Effective Effort by Fishery for North Pacific Albacore, 1961-81

Year	Japan longline (hooks x 10^6)	Japan[1] pole-and-line (days)	Japan[1] pole-and-line (poles x 10^3)	U.S.[1] effort (days)
1952	283.0			
1953	311.1			
1954	409.6			
1955	395.3			
1956	389.1			
1957	346.4			
1958	384.3			
1959	373.7			
1960	455.5			
1961	432.0	4.235		25.255
1962	309.0	1.209		27.464
1963	259.0	4,200		31.456
1964	232.4	3.478		30.355
1965	242.7	6.628		24.945
1966	276.8	3.843		25.756
1967	434.8	5.005		26.453
1968	355.8	3.108		29.175
1969	361.2	6 447		28.528
1970	253.2	3.958		20.165
1971	255.2	7.631		44,015
1972	186.7	9.695	227.8	67.319
1973	173.5	12.685	287.8	32,031
1974	153.8	9.421	226.4	39.748
1975	158.1	8.766	204.5	35.449
1976	227.2	13.921	278.9	38.445
1977	256.2	10.609	203.4	32.292
1978	252.8	16.725	321.9	32.111
1979	278.7	12.761	252.3	17.924
1980	203.0	*	*	28.418
1981	*	*	*	20.945

[1] Japanese pole-and-line days are not the same as U.S. effort days
*Data not available.

where oceanographic processes and weather conditions strongly influence fish availability and catchability. Further, stock recruitment processes are not understood, and many questions about stock structure remain unanswered. As pointed out in past workshops, these subjects should be placed high on the research agenda of the participating laboratories. In the meantime, sensitivity analyses are needed to better define the robustness of current assessment procedures and the direction and magnitude of possible biases.''

STOCK STRUCTURE AND MIGRATION PATTERNS

There is a growing body of evidence (Brock 1943; Laurs and Lynn 1977; Laurs and Wetherall 1981) that North Pacific albacore are not as homogeneous as usually assumed (Clemens 1961; Otsu and Uchida 1963). Results from recent tagging studies (Table 4) suggest that at least two substocks constitute the North Pacific albacore population and that these substocks have different migratory patterns (Laurs and Nishimoto 1979). Fish belonging to a proposed northern substock migrate between the eastern and western North Pacific, causing an exchange of fish between the U.S. fishery north of about 40°N, the Japanese livebait and gill net fisheries, and the foreign longline fisheries west of 180°. The proposed southern group of fish has a different migration scheme from that of the northern group, and appears to enter the U.S. fishery south of about 40°N, and the longline fisheries east of 180°. Only a very small proportion of the southern group of fish appears to migrate between the eastern and western Pacific and enter the Japanese pole-and-line or gill net fisheries. Also, during a given fishing season there is virtually no exchange of fish in the U.S. fishery between the northern and southern groups, although there is a small amount of interannual exchange.

Laurs and Wetherall (1981) found that the growth rate of North Pacific albacore recaptured either off the coast of North America north of 40°N or in the western North Pacific off Japan was significantly lower than that for tagged fish recovered off North America south of 40°N during 1972-78. The differences in growth rate are consistent with differences in length frequencies of albacore caught off North America north and south of 38°N during the period when most recoveries were made (Laurs and Lynn 1977) and during earlier years (Brock 1943). Thus a variety of types of information including tag and recapture data, growth-rate analyses, and differences in size composition of fish caught in the U.S. fishery support the hypothesis that the North Pacific albacore is not a homogeneous population, but rather that there are at least two substocks.

DETERMINATION OF ABSOLUTE AGE

A major void in our understanding of albacore biology is an understanding of true size and age structure. The daily ring increment method for aging fishes (Pannella 1971) offers great promise for determining absolute age and growth rates for albacore. Results from an experiment with tetracycline injection at time of tagging and release have verified that daily rings are laid down on the otolith of the albacore (Laurs and Nishimoto 1981). The method is being applied to albacore otoliths, and valid data on absolute age and size structure will be available in the near future. Preliminary results indicate that the length at first birthday is about 35 to 40 cm FL.

INFLUENCE OF OCEANOGRAPHIC CONDITIONS ON ALBACORE

There is ample evidence that the migration routes and small-scale movements of albacore are markedly influenced by oceanographic conditions. For example, albacore fishing grounds in the western Pacific have been linked to oceanic fronts (Uda 1973). Also, the

TABLE 3

CPUE[1] Statistics for Major North Pacific Albacore Fisheres, 1961-80

Year	Japan Pole-and-line Fishing days	Japan Pole-and-line Poles	United States jig	Japan longline "Young" area[2]	Japan longline "Main spawning" area[3]	Japan longline Entire area[4]
1961	4.40		69.17	0.55	0.14	0.25
1962	7.22		124.59	0.67	0.14	0.30
1963	6.29		132.09	0.68	0.19	0.32
1964	6.86		97.61	0.90	0.19	0.40
1965	6.26		89.07	0.70	0.25	0.33
1966	5.94		90.45	1.20	0.27	0.54
1967	6.09	259	126.83	0.88	0.29	0.40
1968	5.34	227	135.23	0.84	0.29	0.38
1969	4.95	211	112.57	0.60	0.31	0.28
1970	6.13	261	127.39	0.66	0.27	0.31
1971	6.94	295	96.68	0.43	0.22	0.21
1972	6.25	266	61.08	0.63	0.30	0.30
1973	5.49	242	82.89	0.85	0.30	0.38
1974	7.81	325	105.17	0.64	0.30	0.34
1975	5.98	255	99.81	0.46	0.21	0.23
1976	6.13	306	69.22	0.66	0.21	0.30
1977	3.01	157	59.90	0.60	0.14	0.26
1978	3.58	186	86.80	0.52	0.17	0.23
1979	3.50	187	45.41	0.53	0.21	0.24
1980	4.44	268	36.78	0.72	0.26	0.33
1981	3.05	—	80.11	—	—	—

[1] Unit: MT/vessel-day and kg/pole-day for Japan pole-and-line; fish/vessel-day for United States jig; fish/100 hooks for Japan longline
[2] "Young" area is 25°-45°N from October to March and 30°-45°N from April to September.
[3] "Main spawning" area: 10°-25°N
[4] Entire area: 0°-45°N

seasonal migration of albacore into North American coastal waters has been found to be associated with the Transition zone and its frontal boundaries (Laurs and Lynn 1977). In addition, oceanographic conditions play an important role in the local concentrations and movements of albacore in U.S. coastal waters. Using concurrent ultrasonic tracking of free-swimming fish and oceanographic sampling, Laurs et al. (1977) found that albacore tend to aggregate in the vicinity of coastal upwelling fronts, presumably to feed, and to move away from the area when upwelling ceases and the front is no longer present.

TABLE 4

Summary of Where Tagged Albacore Were Recovered Relative to Area of Release

Area of Recovery	Area of release Inshore south 40°N	Area of release Inshore north 40°N	Area of release Offshore 130°W
Inshore south 40°N	78%	7% (0.8)*	31%
Inshore north 40°N	5% (0.4)*	32%	30%
Japanese livebait	4.5%	48%	21%
Japanese longline			
East of 180°	2%	0%	0.5%
West of 180°	0%	2.5%	1.5%
Unknown			
U.S. fishery	11.5%	9.5%	16%
Japanese fishery	0%	1%	0%

*Percentage recovered same year of release.

Very little has been published concerning relationships between oceanographic conditions and the vertical distribution of albacore. However, Clemens (1961) hypothesized that the thermocline acts as a barrier to albacore and that variations in albacore availability in waters off the U.S. are related to variations in the topography of the 14°C (58°F) isotherm.

Laurs et al. (1980) examined the vertical distribution of free-swimming albacore, measured by acoustic telemetry, in relation to ocean vertical thermal structure, measured concurrently with expendable bathythermographs (XBTs). We found that tracked fish spend little time in the upper layer, where it has been generally believed immature albacore (< about 6 years old) are distributed. The fish spent much of their time in the thermocline and were often well below the thermocline. Fish were found in waters 2° to 5°C (4° to 10°F) below what has been thought to be the optimal temperature range for albacore (Clemens 1961). Also, in some instances the tracked fish underwent changes in depth distribution resulting in temperature changes of as much as 5°C (10°F) within 10- to 30-minute periods.

Recently Laurs and Austin (unpublished results) investigated the small-scale migration patterns of albacore in relation to oceanic frontal boundaries using ocean color and infrared satellite data collected contemporaneously with observations made from ships at sea. NIMBUS-7 Coastal Zone Color Scanner (CZCS) and NOAA 6 satellite AVHRR infrared data were collected in conjunction with field experiments where acoustic telemetering methods were used to track the horizontal and vertical movements of free-swimming albacore, and XBT observations were made to determine subsurface ocean thermal structure. Three albacore were tracked for approximately 24 hours and one for about 15 hours. The results showed that (1) total distances tracked ranged from about 40 to 60 km, with all fish remaining in the same parcel of warm water that was separated from waters to the north, south, and inshore by about a 2°C (4°F) temperature gradient as shown by infrared thermal imagery; (2) tracked fish spent most of the time in waters within and below the thermocline, and only small amounts of time in the upper mixed layer; (3) the fish exhibited marked vertical excursions in depth, with the range being larger during the day than at night; (4) the fish spent most time in waters with temperatures considerably lower than what has been generally believed to be the preferred temperature range for albacore; and (5) when changing depth, the fish, frequently within a 20-minute period, passed through a vertical gradient of temperature amounting to 6° to 7°C (12° to 15°F), or about 3+ times greater than the horizontal temperature gradient at the surface indicated by ship measurements and the infrared thermal imagery.

These findings indicate that the reasons that tunas aggregate on the warm side of surface temperature fronts—an economically significant phenomenon that has been observed on scientific cruises and is well known by fishermen—may not be related to thermal-physiological mechanisms (Neill 1976). Instead, Laurs and Austin speculate that one or more behavioral mechanisms related to feeding may be responsible. Ocean color measurements made by the CZCS in conjunction with the tracking study and with catches made by commercial fishing vessels[3] provide data that support this hypothesis.

The diffuse attenuation coefficient (*k*), a measure of water clarity measured by the CZCS, showed a gradient nearly coincident with the sea-surface temperature gradient pattern, with lower values of *k* in the warm waters and higher values in the cooler waters. The distribution of color boundaries indicated by the ratio of blue:green color bands measured by the CZCS was also similar to the gradient pattern observed in the diffuse attenuation coefficient (*k*).

The results show that the albacore remained in water that had higher clarity than adjacent waters. This suggests that water clarity's effect on the tuna's ability to see its prey may play a key role in the mechanisms underlying the aggregation of tunas on the warm, clear side of ocean surface thermal fronts.

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SAMPLE SIZE FOR ESTIMATING DOLPHIN MORTALITY ASSOCIATED WITH THE TUNA FISHERY

NANCY C. H. LO, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038

Abstract: Dolphin (*Stenella* spp., *Delphinus delphis*) mortality caused by U.S. tuna purse seiners in the eastern tropical Pacific has been monitored under a quota system since 1976. A stratified ratio estimator (kill-per-day) has been used to measure the kill rate during the year. Vessel trips are stratified by fishing time period. The mortality data from 1976 through 1978 suggest a sample-size procedure based on the coefficient of variation rather than on the absolute variance of kill data. The sample size for each stratum is computed according to the desired precision of the stratum estimates rather than by allocation of a yearly sample size. The probability that the estimated mortality exceeds the quota, when in fact the quota is higher than the true mortality, is computed. This sample-size procedure is recommended for data that have a standard deviation proportional to the mean and the situation where the estimate within stratum is as important as the overall estimate.

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Yellowfin tuna (*Thunnus albacares*) are often associated with dolphins (e.g., *Stenella attenuata*, *S. longirostris*, etc.) in the eastern tropical Pacific (ETP) and fishermen have used this association to catch fish. A purse seine net (McNeely, Pac. Fish. 59[7]:27–58, 1961) is used to encircle an entire aggregation of tuna and dolphin in an operation called a "dolphin set." During the dolphin set, dolphins encircled together with tuna are often entangled in the nets and accidentally drown.

The purse seine fishing technique in the ETP was first introduced to the tuna fleet in the early 1960's. Currently there are about 100 purse seiners, each with a carrying capacity of over 400 short tons, in the U.S. fleet. Each vessel averages 3 or 4 trips a year and the entire fleet is expected to make about 350 trips resulting in 6,000 dolphin sets each year.

The fishing area is from 40°S to 40°N latitude, 150°W longitude to the west coast of the American continent. The yellowfin tuna catch in the area known as the Commission Yellowfin Regulatory Area (CYRA) is regulated by an allowable tuna catch set by the Inter-American Tropical Tuna Commission (IATTC). After the allowable tonnage catch of yellowfin tuna has been taken (usually by Jul) in the CYRA, most vessels fish outside the CYRA and mainly target on tuna associated with dolphins. Hence, higher dolphin mortality is expected after July.

The National Marine Fisheries Service (NMFS) initiated an observer program in 1971 through which NMFS-trained biological technicians are placed aboard randomly selected U.S. tuna vessel trips to collect data on dolphin mortality and biological information. Kill rates of the observed and unobserved vessels are assumed to be similar because the bias, if it exists, cannot be measured.

Until 1977, it was estimated that over 100,000 dolphins were killed each year. In 1976, the NMFS established an annual quota on maximum allowable kill of dolphins by U.S. fishermen. The objective of this paper is to discuss a sample-size procedure for a stratified-ratio estimator of the incidental dolphin mortality on a real-time basis during the year with vessel trips stratified by fishing time period. This procedure accounts for decreasing mortality levels in recent years resulting from gear improvement, as well as the high associ-

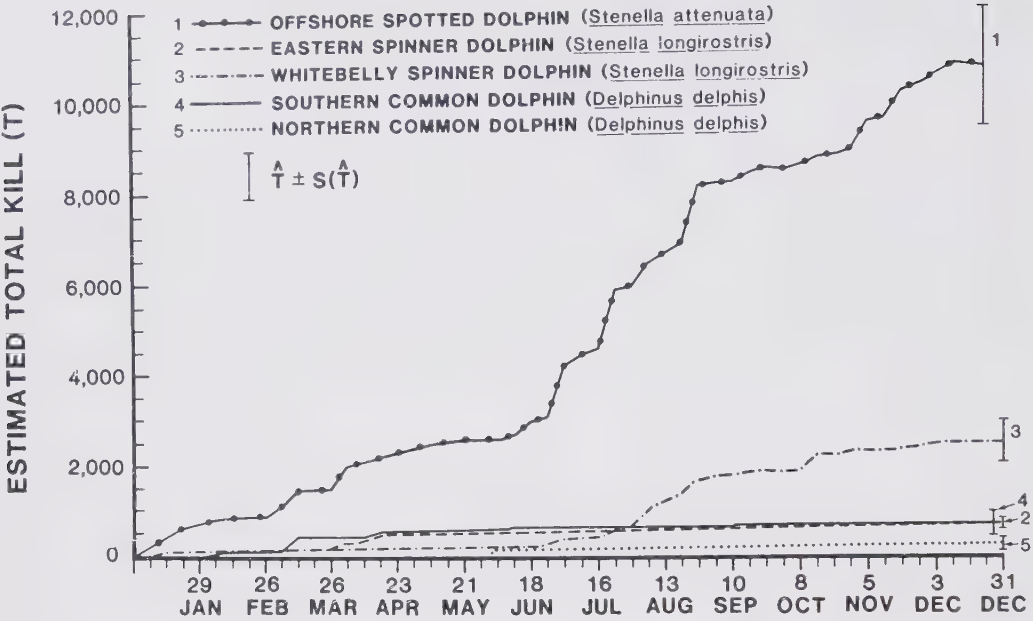

Fig. 1. Weekly estimates of cumulative mortality by management stock of dolphins, 1978.

ation of mean and standard deviation of the kill. This procedure is based on the coefficient of variation (CV) of the estimators of kill rates rather than on their absolute variances (Cochran, Sampling techniques, J. Wiley & Sons, New York, N.Y., 1977).

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MORTALITY MONITORING PROGRAM

The Marine Mammal Protection Act of 1972 and a court ruling in 1976 required the NMFS to set an annual quota for the incidental take of dolphins by the American tuna fleet. The quota is an attempt to reduce incidental dolphin mortality associated with tuna fishing by U.S. purse seiners in the ETP. For 1976–80, the annual quotas were 78,000, 62,000, 52,000, 42,000, and 31,000, respectively. After 1976, the quotas were set by species (stock). If the quota of any species (stock) is reached, the yellowfin tuna fishing on that species (stock) is prohibited for the remainder of the year (U.S. Dep. Commer., Fed. Reg. Pt. 3, 42[40]:12010–12020, 1977).

Beginning in 1976, biological technicians aboard tuna vessels reported cumulative mortality data each week by radio. The observed kill-per-day is used to estimate the total mortality for the entire fleet on a real-time basis (Fig. 1). Many kill ratios have been used to measure kill levels, e.g., kill-per-set, kill-per-tonnage-of-yellowfin tuna-catch. Kill-per-day was chosen to estimate total kill during the year because data on total days are available throughout the year whereas tonnage of yellowfin tuna catch and total number of dolphin sets are not known until the end of the year (Lo et al., Fish. Bull. 80:396–400, 1982).

DOLPHIN MORTALITY ESTIMATION

The simplest estimate of total mortality to a given point in time would be the total mortality for the observed vessels inflated by the ratio: number of vessels in the fleet divided by number of observed vessels. However, because each vessel does not make the same number of fishing trips and trips vary in length, kill-per-trip or kill-per-day may be used to reduce the variability in the estimate of total mortality. The kill-per-day statistics have been used for monitoring the mortality against the quota. In a stratified sampling scheme, the estimated total mortality based on kill-per-day can be derived as described below.

The sampling units are vessel trips stratified by fishing time period to account for both average kill and the availability of kill differing among seasons within a year. The season is determined by the availability of yellowfin tuna and the allowable catch tonnage for yellowfin tuna set by the IATTC.

A year is divided into 3 periods (Jan–Mar, Apr–Jun, Jul–Dec). The number of trips starting within each period is considered as the total number of vessel trips within stratum (N_i, $i = 1, 2, 3$). The trip data from previous years are used to predict N_i for the current year. The vessel trip distribution (N_i) with percentage in parentheses in 1978 was

$i =$ 1	2	3	
(Jan–Mar)	(Apr–Jun)	(Jul–Dec)	Total
115 (35)	94 (28)	122 (37)	331 (100).

Note that for the ith time period:

n_i = number of observed trips,
x_{ij} = number of dolphins killed by the jth observed (sampled) vessel trip,
d_{ij} = number of days at sea (duration) of the jth observed vessel trip,
N_i = total number of vessel trips,
$f_i = n_i/N_i$ = sampling intensity,
D_i = total number of days at sea by the fleet,
T_i = total kill,
r_i = kill-per-day $= T_i/D_i = \mu_i(x)/\mu_i(d)$, where $\mu(\cdot)$ is the true mean, i.e., $\mu_i(x) = T_i/N_i$ and $\mu_i(d) = D_i/N_i$, and
$T_i = D_i r_i$.

Total kill for the year is the sum of total kill within each time period, i.e.,

$$T = \sum_i T_i = \sum_i D_i r_i$$

and

$\hat{T}_i$ = the estimated total kill in the ith time period $= D_i \hat{r}_i$.

To compute $\hat{T}_i$, it remains to choose appropriate estimates $\hat{r}_i$ for r_i, the "average kill-per-day" in the ith stratum. The data obtained from the observed vessels are number of kills x_{ij} by the jth vessel trip in the ith stratum. It is assumed that r_i is related to the kill x_{ij} by

$$x_{ij} = r_i d_{ij} + e_{ij},$$

where e_{ij} has mean zero and variance σ_i^2:

$$\sigma_i^2 = \sum_{j=1}^{N_i} (x_{ij} - r_i d_{ij})^2/N_i.$$

The estimator of the form

$$\hat{r}_i = \sum_j x_{ij} / \sum_j d_{ij} = \bar{x}_i/\bar{d}_i$$

is used because $\hat{r}_i$ is a consistent estimator of r_i in a sense that

$$\lim_{n_i \to N_i} \hat{r}_i = r_i.$$

Moreover, 1977 data indicated a linear relationship between kill (x_{ij}) and days at sea (d_{ij}) (Fig. 2), and the variance of kill around the line is proportional to number of days at sea (d_{ij}). For this model

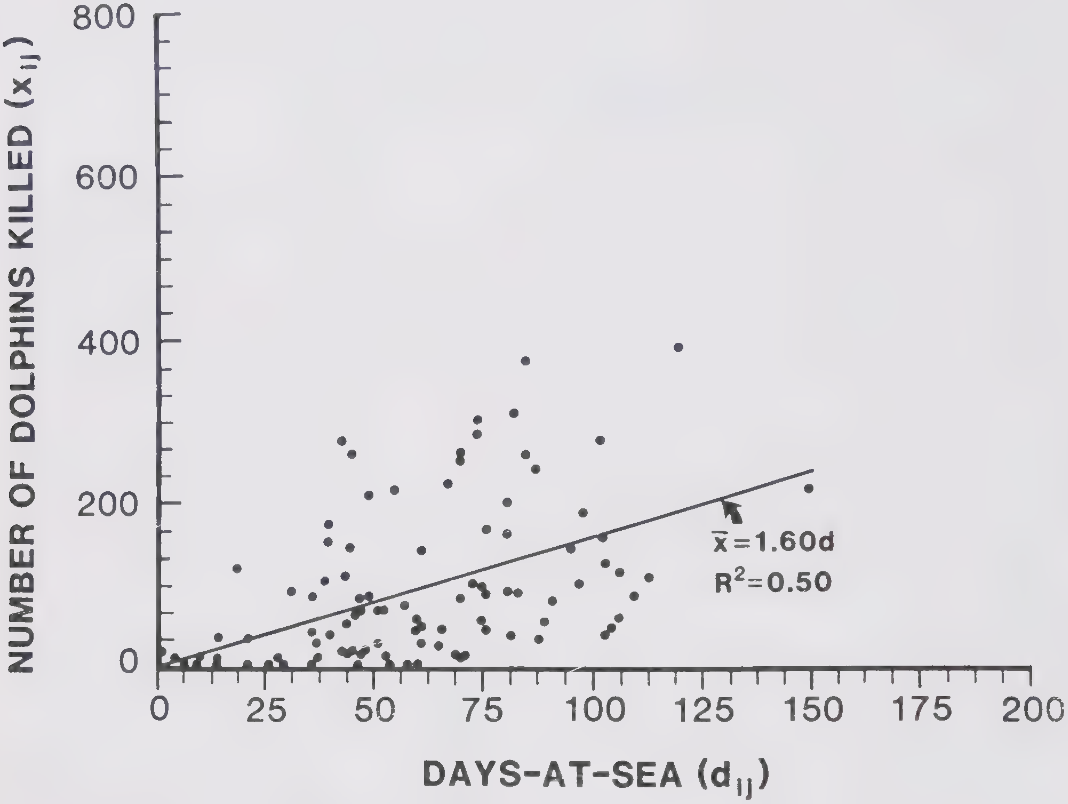

Fig. 2. Linear relationship of dolphin kill and days at sea, 1977.

$$\hat{T} = \sum_i D_i \hat{r}_i = \sum_i D_i \sum_j x_{ij} / \sum_j d_{ij}. \qquad (1)$$

The variance of $\hat{r}_i$ according to Cochran (1977) is

$$\sigma^2(\hat{r}_i) = (1 - f_i)\frac{1}{n_i}\,\frac{1}{\mu_i^2(d)}\sigma_i^2,$$

where σ_i^2 is estimated by

$$s_i^2 = \sum_{j=1}^{n_i} (x_{ij} - \hat{r}_i d_{ij})^2/(n_i - 1). \qquad (2)$$

Thus $\sigma^2(\hat{r}_i)$ is estimated by

$$s^2(\hat{r}_i) = (1 - f_i)\,\frac{1}{n_i}\,\frac{1}{\mu_i^2(d)} s_i^2 \qquad (3)$$

and the sample variance of $\hat{T}$ is, assuming that $\hat{T}_i$ and $\hat{T}_j$ are independently distributed:

$$s^2(\hat{T}) = \sum_i D_i^2 s^2(\hat{r}_i). \qquad (4)$$

SAMPLE SIZE DETERMINATION

Determination of sample size for a stratified sampling scheme could be based on the magnitude of both the mean and variance of kill of each stratum obtained in the previous years. However, this procedure is applicable only when the within-stratum variability of kill is independent of the average kill-per-trip and thus may not be valid for dolphin mortality estimation.

One characteristic of dolphin mortality data was the high correlation between mean kill and standard deviation. Because the mean kill varies for vessels with different gear type, carrying capacities, and fishing time periods, the observed vessels in 1976–78 were grouped according to these categories. To illustrate the high correlation between mean and standard deviation of dolphin mortality, average kill-per-trip ($\bar{x}$) and standard deviation ($\bar{s}$) were computed for each group and fitted by simple linear regression through the origin: $s = 1.37\bar{x}$ and $R^2 = 0.93$. Note that the regression coefficient 1.37 ($=s/\bar{x}$) was also an estimate of the coefficient of variation of the kill data ($\mathrm{CV} = \sigma/\mu$) over a 3-year period.

Kill rates have dropped each year as a result of the dolphin mortality reduction effort; the unstratified kill-per-trip estimates for 1976, 1977, and 1978 were approximately 200, 106, and 63, respectively. The corresponding standard deviations of the kill were 290, 120, and 124. Thus, the estimate of individual yearly coefficient of variation was 1.45, 1.13, and 1.97, respectively. To obtain the same level of precision in each year (e.g., 95% CI = estimate ± 2 × 0.10 × estimate), more observed trips would be required for 1978 than for 1977 even though the absolute variances for 1978 and 1977 were similar. The fact that yearly distributions of the observed mortality are skewed and that the standard deviation is usually larger than the mean necessitates large sample sizes.

A stratified sampling scheme usually attempts to maximize the precision of the estimate of the population total over all strata. For dolphin mortality, however, the mortality estimates in the 1st 2 periods are also important because they must be compared directly with the yearly quota. Therefore, the number of observed trips should be determined within each stratum rather than by the standard method of determining n, total number of observed trips, which is allocated to each stratum (Cochran 1977).

An individual stratum is each fishing period within a year (e.g., Jan–Mar). Within each stratum, the number of observed trips (sample size) was calculated. For stratum i, the sample size required for a desired $\mathrm{CV}(\hat{T}_i)$ was written in terms of the estimated $\mathrm{CV}(x_{ij})$ available from historical data: $\mathrm{CV}_i = s_i/\bar{x}_i$ and s_i is the sample standard deviation of kill computed according to eq. (2).

Using eqs. (1) and (3) (Cochran 1977),

$$\begin{aligned}\mathrm{CV}(\hat{T}_i) &= \frac{\sigma(\hat{T}_i)}{\mu(\hat{T}_i)} \doteq \frac{s(\hat{T}_i)}{\hat{T}_i} = \frac{s(D_i\hat{r}_i)}{D_i\hat{r}_i} = \frac{s(\hat{r}_i)}{\hat{r}_i}\\ &= \left[\frac{1}{n_i}(1-f_i)\right]^{\frac{1}{2}} \frac{s_i}{\mu_i(d)}\,\frac{1}{\hat{r}_i}\\ &\doteq \left[\frac{1}{n_i}(1-f_i)\right]^{\frac{1}{2}} \frac{s_i}{\bar{x}_i}\\ &= \left[\frac{1}{n_i}(1-f_i)\right]^{\frac{1}{2}} \mathrm{CV}_i. \end{aligned} \tag{5}$$

Solving eq. (5) for n_i,

$$\begin{aligned} n_i &= \left\{\frac{1}{N_i} + \left[\frac{\mathrm{CV}(\hat{T}_i)}{\mathrm{CV}_i}\right]^2\right\}^{-1}\\ &= \left(\frac{1}{N_i} + \phi_i{}^2\right)^{-1}, \end{aligned} \tag{6}$$

where $\phi_i = [\mathrm{CV}(\hat{T}_i)]/\mathrm{CV}_i$. $\mathrm{CV}(\hat{T}_i)$ is specified by the user and CV_i is estimated from past data. The sample size (n_i) is independent of the absolute value of mean and variance. For dolphin mortality estimation, the mean and variance of kill change each year. Equation (6) is used to compute the sample sizes.

Sample size for the entire year is the sum of n_i ($i = 1, 2, 3$). The number of trips per stratum as estimated from eq. (6) depends on total number of trips (N_i), and the ratio (ϕ_i) of $\mathrm{CV}(\hat{T}_i)$ and CV_i. The min-

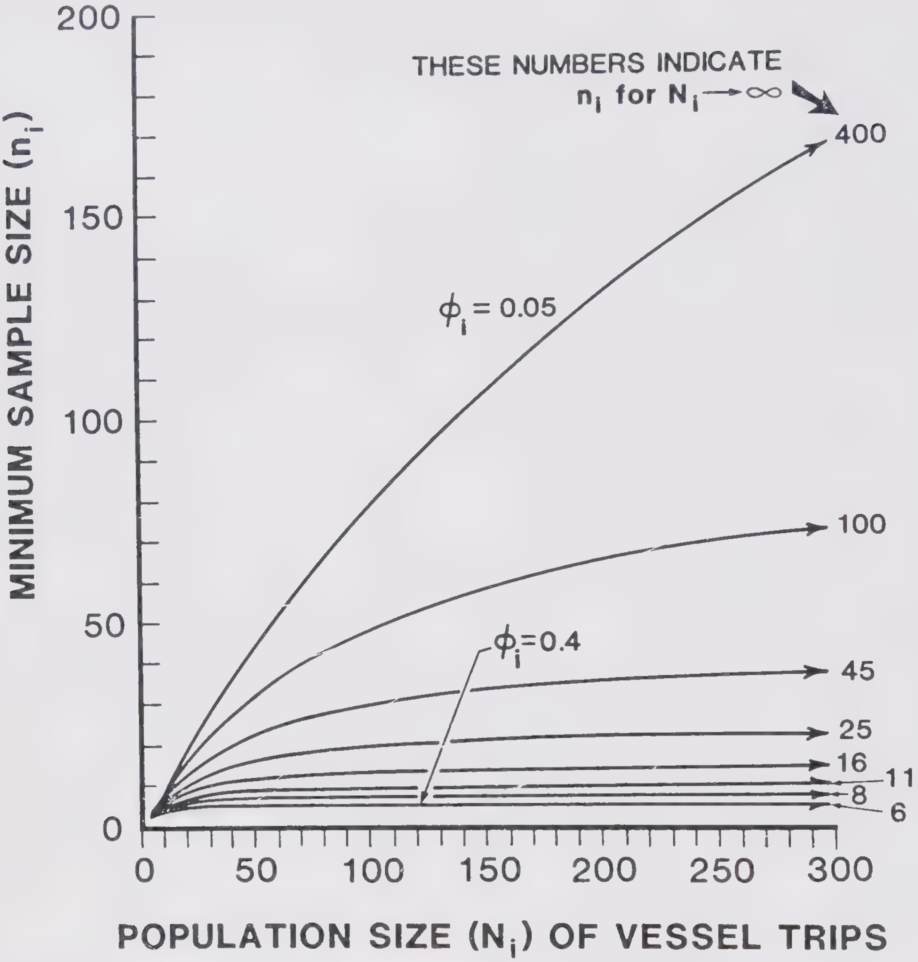

Fig. 3. Minimum sample sizes for population sizes (N_i) and ϕ_i, ϕ_i = 0.05 (0.05) (0.40).

imum number of observed trips was computed for N_i up to 350 and $\phi_i = 0.05$ (0.05) (0.4) (Fig. 3).

PROBABILITY THAT ESTIMATED MORTALITY EXCEEDS ESTABLISHED QUOTA

The annual quota is set for each species (stock). For any 1 species (stock), if the estimated mortality ($\hat{T}$) exceeds its quota (Q), i.e., $\hat{T} > Q$, then the yellowfin tuna fishing associated with that species (stock) is prohibited for the remainder of the year. Sample sizes for monitoring purposes were evaluated based on the probability that the estimated total mortality exceeds or falls short of an established quota when in fact the true total mortality is below or above the quota. If the true total mortality is at or slightly below quota levels, overestimated mortality is likely but undesirable. When the true total mortality is much below the quota, observed trips may be reduced because only crude estimates of mortality would be required. This probability of risk depends on the sampling distribution of the estimated total mortality, which is a function of sample size and the variation of the data, measured by coefficient of variation. Under a stratified sampling scheme the probability of an erroneous decision (P) is denoted by:

$$P[\hat{T} > Q \mid T < Q, n_i, \mathrm{CV}_i, \mathrm{CV}(\hat{T}_i)] \text{ or } P[\hat{T} < Q \mid T > Q, n_i, \mathrm{CV}_i, \mathrm{CV}(\hat{T}_i)],$$

where T = actual total mortality by all vessel trips,
$\hat{T}$ = estimated total mortality,
Q = quota on allowable total mortality of dolphins,
n_i = total number of observed trips within stratum i, and
CV_i and $\mathrm{CV}(T_i)$ are defined as before.

Assuming the distribution of total mortality during the year is proportional to the yellowfin catch on dolphin over time, it is clear that $T = T(g_1 + g_2 + g_3) = T_1 + T_2 + T_3$, where g_i is the proportion of yellowfin catch on dolphin in the ith time period during the year and is predicted based on past data, $\sum_i g_i = 1$.

Likewise, $\hat{T} = \hat{T}_1 + \hat{T}_2 + \hat{T}_3$

and

$$\sigma^2(\hat{T}) = \Sigma\, \sigma^2(\hat{T}_i) = \Sigma\, T_i^2 \mathrm{CV}^2(\hat{T}_i) = T^2\, \Sigma\, g_i^2 \mathrm{CV}^2(\hat{T}_i).$$

If it is assumed that $\hat{T}$ is normally distributed with mean T and variance $\sigma^2(\hat{T})$ estimated by $s^2(\hat{T})$, then

$$\begin{aligned} &P[\hat{T} > Q \mid T < Q, n_i, \mathrm{CV}_i, \mathrm{CV}(\hat{T}_i)] \text{ or} \\ &P[\hat{T} < Q \mid T > Q, n_i, \mathrm{CV}_i, \mathrm{CV}(\hat{T}_i)] \\ &= 1 - \Phi\left[\frac{|Q - T|}{\sigma(\hat{T})}\right] \\ &= 1 - \Phi\left\{\frac{|Q - T|}{T[\Sigma\, g_i^2 \mathrm{CV}^2(\hat{T}_i)]^{\frac{1}{2}}}\right\}, \end{aligned} \tag{7}$$

where $\Phi(y)$ is the probability that a standard normal random variable exceeds y. Using eq. (5)

$$\begin{aligned} \mathrm{CV}(\hat{T}) &= \frac{\sigma(\hat{T})}{T} \doteq \frac{T[\Sigma\, \mathrm{CV}^2(\hat{T}_i) g_i^2]^{\frac{1}{2}}}{T} \\ &= \Sigma\, [\mathrm{CV}^2(\hat{T}_i) g_i^2]^{\frac{1}{2}} \\ &= h[\Sigma\, g_i^2]^{\frac{1}{2}} \end{aligned} \tag{8}$$

if we choose $\mathrm{CV}(\hat{T}_i) = h$ for all i.

Thus, for a desired $\mathrm{CV}(\hat{T}_i) = h$ or n_i and given values of T, CV_i, g_i, and N_i, the probability P in eq. (7) can be computed. $\mathrm{CV}(\hat{T})$ may be obtained by eq. (8).

RESULTS

The sample size n_i for 1979 vessels was computed to illustrate the technique. The 1978 trip data were used to predict 1979 vessel trips: the trips per vessel and the trip distribution during the year, e.g., the number of trips starting within each period (N_i, i = 1 [Jan–Mar], 2 [Apr–Jun], and 3 [Jul–Dec]).

At the end of 1978, 86 vessels were anticipated to be fishing in 1979. The average number of trips per vessel is 3.18 and the estimated trip distribution for the 3 periods is 35, 28, and 37%, respectively. Therefore,

$$\begin{bmatrix} N_1 \\ N_2 \\ N_3 \end{bmatrix} = 86 \times 3.18 \times \begin{bmatrix} 0.35 \\ 0.28 \\ 0.37 \end{bmatrix} = \begin{bmatrix} 95 \\ 77 \\ 101 \end{bmatrix}.$$

Reasonable values of $\mathrm{CV}(\hat{T}_i)$ to consider are 0.10, 0.15, 0.20, and 0.25. CV_i is difficult to predict during any particular time period. However, using the range of CV_i observed in the past as a guideline, CV_i between 1.0 and 2.0 are probably representative. Thus, observed trips are allocated for 1979 (Table 1). A total of 273 trips was predicted for 1979; the minimum number of observed trips ranged from 41 to 223 depending on the required degree of precision of the estimates and the assumed variation of the data.

This sampling scheme first determines the sample size within stratum, and the

Table 1. Minimum number of observed trips (n_i) needed for each period to obtain mortality estimated within stratum with levels of precision (CV[$\hat{T}_i$] = 0.10, 0.15, 0.20, and 0.25) based on data with 3 levels of variation (CV_i = 1.00, 1.50, and 2.00). (Equation 6).

Time period (i)	N_i	CV($\hat{T}_i$)											
		0.10			0.15			0.20			0.25		
CV_i		1.00	1.50	2.00	1.00	1.50	2.00	1.00	1.50	2.00	1.00	1.50	2.00
ϕ_i		0.10	0.07	0.05	0.15	0.10	0.08	0.20	0.13	0.10	0.25	0.17	0.13
1	95	49	65	77	30	49	59	20	36	49	14	26	36
2	77	44	56	65	28	44	52	19	33	44	13	25	33
3	101	50	68	81	31	50	61	20	37	50	14	27	37
Totals	273	143	189	223	89	143	172	59	106	143	41	78	106

yearly sample size is the sum of stratum sample sizes (Table 1). Minimum sample sizes for other combinations of N_i and ϕ_i can be obtained from eq. (6) or Fig. 3.

The probability that $\hat{T}$ exceeds Q was calculated for the case where $\hat{T} < Q$ because estimates of historical kill rates indicated that mortality was below the 1979 quota (Table 2). Based upon the 1978 yellowfin catch on dolphin distribution over time (i.e., $g_1 = 0.28$, $g_2 = 0.24$, and $g_3 = 0.48$; eq. 8) and the sample-size determination for 1979 where the aggregate quota was 41,610, a table of risk was constructed (i.e., the probability of closing the season before the quota was reached) (Table 3). This table indicates the effect of sample sizes for $CV_i = 1.0$, 1.5, and 2.0 and CV($\hat{T}_i$) = 0.10, 0.15, 0.20, and 0.25.

For example, when the coefficient of variation of the mortality data within stratum CV_i is 1.5, a sample size of 143 is needed to arrive at $\hat{T}_i$ with CV($\hat{T}_i$) = 0.15 (Table 1). The probability that the estimated total mortality ($\hat{T} = \sum_{i=1}^{3} \hat{T}_i$) exceeds the quota depends on the true total mortality. The numerical study indicates that if the true mortality is below 30,000, the estimated mortality rarely exceeds the quota of 41,610 for sample sizes greater than 40. If the true mortality is 40,000, the sample size has to be greater than 140 to guarantee the probability to be less than 25%. Because the dolphin mortality has been monitored by species (stock) since 1977, the P values were also computed for 1 major species of offshore spotted dolphin (*Stenella attenuata*) involved in the fishery. The quota in 1979 was 28,400 spotted dolphins. For a given sample size, the P value for a particular species is greater than that of the aggregate total mortality (Table 3).

Table 2. The predicted annual kill of dolphins based on historic (1971–76) yellowfin tuna catch on dolphin and kill-per-ton.

	Yellowfin catch (short ton)	Kill-per-ton	Predicted kill
Max	132,000	0.31	40,920
Min	99,000	0.25	24,750
Mean	117,000	0.28	32,760

DISCUSSION

The sample size determination used in this paper differs from the conventional approach for stratified sampling schemes in 2 respects: (1) coefficient of variation (CV) is used rather than standard deviation (σ), and (2) sample size for each stratum (n_i) is determined and the sum of n_i is the total sample size for the entire year (n).

Basing sample size on the coefficient of variation is preferred for the situation where standard deviation and mean are highly correlated because CV is independent of mean level whereas σ varies with

Table 3. Probability of estimated dolphin mortality ($\hat{T}$) reaching the quota when the true mortality is below quota of aggregate (41,610) and spotted (28,400) dolphins.

$CV(\hat{T})$ $CV(\hat{T}_i)$	0.06 0.10			0.09 0.15			0.12 0.20			0.15 0.25		
CV_i r^a	1.0 143	1.5 189	2.0 223	1.0 89	1.5 143	2.0 172	1.0 59	1.5 106	2.0 143	1.0 41	1.5 78	2.0 106
True mortality (T)												
20,000 (A)[b]		*			*			*			*	
14,000 (S)		*			*			*			*	
25,000 (A)		*			*			*			*	
17,500 (S)		*			*			*			*	
30,000 (A)		*			*			*			0.01	
21,000 (S)		*			*			*			0.01	
35,000 (A)		0.00[c]			0.02			0.06			0.10	
24,000 (S)		0.00			0.04			0.09			0.15	
40,000 (A)		0.25			0.34			0.37			0.40	
28,000 (S)		0.40			0.44			0.45			0.46	

* $P \leq 0.001$.
[a] See Table 1.
[b] A = aggregate, S = spotted dolphins.
[c] $0.001 < P < 0.005$.

the mean and could be misleading. For example, estimates from 2 years with equal CV are considered to be of the same precision yet their standard errors could be entirely different because of the possible difference in their mean levels.

When the estimated total mortality over time is compared with the quota, the estimates within each stratum are as important as the overall estimate. Normally the sample size (n) is computed according to the precision of the overall estimate $CV(\hat{T})$ for the entire year. The sample size for the ith stratum (n_i) obtained by allocation of n could be inadequate for the precision of within-stratum estimate $CV(\hat{T}_i)$ because $CV(\hat{T}_i)$ is greater than $CV(\hat{T})$ (eq. 8). Therefore, to obtain a desired $CV(\hat{T}_i)$, the sample size for each stratum (n_i) should be determined first as opposed to the conventional procedure by which allocation of sample size to each stratum is performed after the sample size is determined.

This procedure of determining sample size is recommended for estimation problems where the standard deviation is proportional to the mean and the precision of the estimates within each stratum is as important as that of the overall estimate. The allocation method based on coefficient of variation rather than on variance is more realistic and generally applicable to the sampling of natural populations where mean and standard deviation are highly correlated.

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GEOGRAPHICAL AND SEASONAL PATTERNS OF LARVAL FISH SPECIES STRUCTURE IN THE CALIFORNIA CURRENT AREA, 1975

VALERIE J. LOEB[1]
San Diego Natural History Museum
P.O. Box 1390
San Diego, California 92112

PAUL E. SMITH AND H. GEOFFREY MOSER
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038

ABSTRACT

Analysis of 1,504 plankton tows from the 1975 CalCOFI cruise year yielded information on geographical and temporal patterns among 204 larval fish taxa. These taxa represented the spawn of fishes from a variety of habitats and water-mass affiliations. The larvae of certain commercially valuable pelagic spawning fishes (anchovy, hake, sardine, jack mackerel, and Pacific mackerel) dominated (75.5% of total larvae); these species are treated separately from the less abundant taxa (further separated into continental shelf, oceanic, and mesopelagic categories and taxa) to permit description of underlying hydrographically related distribution patterns within the California Current area.

The composition and species abundance relations of the ichthyoplankton were similar to those reported from 1955-58. Exceptions were decreased relative abundance of sardine and increased proportions of anchovy larvae in 1975 vs 1955-58.

Anchovy, hake, and jack mackerel larvae were most abundant south of Point Conception. Abundances of rockfishes and bathylagids decreased, while those of flatfishes, myctophids, and gonostomatids increased, from north to south and inshore to offshore. Absolute ichthyoplankton abundance varied by a factor of 10 between January-March (maximum) and September-December (minimum). Anchovy, hake, jack mackerel, rockfishes, sciaenids, myctophids, and bathylagids had January-March abundance peaks; myctophids and gonostomatids had July abundance peaks; flatfishes were most abundant from October-December. Regional ichthyoplankton abundance fluctuations and compositions were related to hydrographic regimes.

The area off northern Baja California marked a transition between predominantly cold-water or subarctic-transition zone species with January-March abundance peaks and predominantly eastern tropical Pacific or warm-water species with summer and fall abundance peaks. This transition zone coincides with a persistent lobe of negative wind stress curl (surface-layer convergence) extending to the coast from offshore waters; this zone may separate biological regimes of California and southern Baja California.

RESUMEN

Los análisis de 1504 colecciones de plancton correspondientes al crucero CalCOFI de 1975, proporcionan información sobre la distribución en espacio y tiempo de 204 taxones de larvas de peces. La puesta de peces procedentes de una variedad de habitats y masas de agua aparece representada en la diversidad taxonómica larval. Las larvas de peces de importancia comercial y de puesta pelágica, *Engraulis mordax* (anchoa), *Merluccius productus* (merluza), *Sardinops caerulea* (sardina), *Trachurus symmetricus* (jurel), eran dominantes, alcanzando el 75.5% del total. Estas especies se estudian en particular y se separan de las especies menos abundantes, clasificadas bajo características taxonómicas y del habitat (plataforma continental, oceánicas y mesopelágicas), para permitir así la descripción de los tipos de distribución en relación con las características hidrográficas dentro de la región de la Corriente de California.

La composición y abundancia de especies del ictioplancton aparecían similares a las presentadas durante el período 1955-58, excepto que en 1975 disminuye la abundancia de larvas de sardina y aumenta proporcionalmente la cantidad de larvas de anchoa.

Larvas de anchoa, merluza y jurel aparecían menos abundantes al sur de Punta Concepción. La abundancia de Scorpenidae y Bathylagidae disminuía, mientras que los peces planos, Myctophidae y Gonostomidae aumentaban de norte a sur y de la costa hacia mar abierto. La abundancia absoluta de ictioplancton fluctuaba en un factor de 10 entre los períodos de Enero-Marzo (máximo) y Septiembre-Diciembre (mínimo). Anchoa, merluza y jurel, Scorpenidae, Sciaenidae, Myctophidae y Gonostomidae aparecían con máximos de abundancia en Julio, y los peces planos eran más abundantes en el período de Octubre-Diciembre. Fluctuaciones en la abundancia regional y la composición del ictioplancton aparecían relacionadas con el régimen hidrográfico.

La zona frente al norte de Baja California marcaba una transición entre aguas predominantemente frias o de la zona subártica- transición, con máximos de abundancia en el período de Enero-Marzo, y especies

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[1] Current address: Moss Landing Marine Laboratories, P.O. Box 223, Moss Landing, CA 95039

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de aguas cálidas, principalmente del Pacífico tropical oriental, mostraban máximos de abundancia en verano y otoño. Esta zona de transición coincide con un lóbulo de remolino persistente de presión eólica negativa (convergencia en el lecho superficial), extendiéndose desde mar afuera hacia la costa. Esta zona puede separar regímenes biológicos de California y la zona sur de Baja California.

INTRODUCTION

The California Current system is a typical eastern boundary current regime (Wooster and Reid 1963; Hickey 1979). The main current is slow, meandering, broad, and indistinct. Embedded in this current are dynamic mesoscale eddies of uncertain origin (Owen 1980), and the current includes water-mass mixtures of diverse origin. The mixed layer can include waters from the (1) North Pacific central water mass, (2) subarctic water mass, (3) Columbia River Plume, (4) subtropical water mass, (5) Davidson Current (a wintertime surface manifestation of the California Undercurrent), and (6) upwelling processes.

The biota of the area also is complex (McGowan and Miller 1980). Invertebrate "holoplankton" species can often be far from their water-mass centers of distribution because of long-range transport; older holoplankton individuals can be far from the reproductive locus of the population. The ichthyoplankton represents a brief phase in a generally longer life cycle, which is in most cases nektonic. Because larval fishes from pelagic spawn are localized at or near the spawning areas of the adults, the analysis of ichthyoplankton in the California Current area can achieve more advanced and precise localization of communities or biological regimes than can analysis of the holoplankton.

To date, most of the descriptive work from the vast set of stations included in the California Cooperative Oceanic Fisheries Investigations (CalCOFI) has concentrated on regional and seasonal characteristics of single oceanographic properties such as current flow, temperature, salinity, and zooplankton volume. The ichthyoplankton has been described only as single species (anchovy, sardine, jack mackerel, hake, individual mesopelagic fish, flatfish, and rockfish species) on distribution charts covering a variety of years. Aside from one paper on the co-occurrence of anchovy and sardine (Ahlstrom 1967) there have been no attempts to characterize the California Current system biota by means of larval fish assemblages.

In this paper we investigate seasonal and geographical distributions within the diverse larval fish assemblage sampled during 1975. We compare the overall composition of this assemblage with that reported from 1955-58. We then divide the ichthyoplankton into various categories based on adult habitats and analyze seasonal abundance relations of these categories (and of their dominant species) within and between pre-established and arbitrary regional divisions.

We emphasize various nonparametric analytical procedures (outlined in Fager 1963) to describe and compare regional ichthyoplankton assemblages. The procedures and results from this study will serve as a basis for subsequent analyses of and comparisons between data sets from other years in the 1951-81 CalCOFI survey. From such analyses we eventually hope to (1) compare variations in larval fish assemblages with variations of reproductive success of commercially valuable fish species; (2) establish the use of changing ichthyoplankton assemblages as indices of general, sustained, and widespread environmental change; and (3) establish the existence of functional relationships between abundances of major fish species and their invertebrate planktonic prey.

METHODS

The present data came from the same 1,504 samples used to describe geographical and seasonal patterns of ichthyoplankton and zooplankton distributions in Loeb et al. 1983a. These samples were from standard CalCOFI plankton tows taken with a l-m diameter net (mesh size, 505 μm) fished from 0-210 m at basic CalCOFI stations and additional inshore stations. Larval fishes were sorted out, identified to the lowest taxon possible, and counted.

Data were formatted by cruise and standard CalCOFI regions. In 1975, 11 regions were "adequately" sampled; "adequate" means that a region was sampled during at least six one-month cruises and was generally represented by > 10 samples per cruise. All regions were sampled in December, January, March, May, and July, and most were sampled in October. Central California regions 4 and 5 were sampled in November rather than October. November data for southern California regions 7, 8, and 9 were used rather than October data because larger numbers of samples were available (Loeb et al. 1983a). Regional data were combined into four latitudinal areas (central California, southern California, northern Baja California, and central Baja California) for broader overviews of patterns of species structure. For region and area locations see Loeb et al. (1983a).

We divide the total ichthyoplankton ("TL") into "PL" (the commercially important pelagic schooling species: anchovy, hake, sardine, jack mackerel, and Pacific mackerel) and "OL" (other larval fish) fractions. These two fractions are treated separately because abundances of the PL (especially anchovy and hake) mask abundance relations of the 200+ other larval fish taxa. The OL taxa are herein further divided into continental shelf ("shelf"), open-ocean epipelagic ("oceanic"), and "mesopelagic" categories for considerations of the major ichthyoplankton components. The shelf category is further divided into "rockfish" (*Sebastes* spp), "flatfish" (Pleuronectiformes), and "other" categories for consideration of regional and seasonal abundance variations.

Larval fish abundances are presented as mean numbers per 10 m^2 sea-surface area (Kramer et al. 1972) and as estimated absolute abundances for each region (mean numbers per 1 m^2 sea surface multiplied by sea-surface area). These latter estimates are summed to provide the total estimated abundances within the CalCOFI survey area by cruise and for all six cruises. As some categories were excluded (e.g., unidentified larvae) the total larval abundances presented here vary slightly from those in Loeb et al. 1983a. Species lists and abundance information for the total CalCOFI area and for each of the 11 regions during 1975 are on file at the Southwest Fisheries Center, La Jolla, California.

We describe species structure using several nonparametric tests. (A) Between-area and between-region comparisons of species percentage composition are made using the Percent Similarity Index (PSI; Whittaker 1975). PSI values compare two species lists based on the relative proportions of individual species within each list. PSI values may range from 0 (no species in common) to 100 (all species in common, and their proportions identical). PSIs are strongly influenced by abundant species. We define as "high" all PSI values > 60, and as "low" values < 40. (B) Comparisons of rank order of abundance of species between sets of data are made using Kendall's tau and concordance tests (Tate and Clelland 1957). Kendall's tau provides a correlation coefficient that is a measure of the similarity between the order of rankings within two data sets. The concordance test is a nonparametric analysis of variance performed on several sets of species' rankings; it is used to test for similarity (nonrandomness) of species' rankings across data sets.

These techniques are used to show similarities in species structure between geographical regions and between seasons. Similarities may occur in the proportions of individual taxa relative to the total ichthyoplankton and in ranks of abundance of individual taxa.

Taxonomic Problems

The 1975 data include 204 ichthyoplankton taxonomic categories: 104 species and 100 higher-level identifications. While many of the abundant larvae (especially the myctophids and bathylagids) have been identified to species, many of the coastal larvae have not. Problems are greatest with the scorpaenids (> 50 species are lumped into the *Sebastes* spp category), the *Citharichthys* category (5 species), the sciaenids (> 10 species), and some subtropical forms. Such multispecies groupings, especially within dominant taxa, impose limitations on analysis of species structure, and geographical or seasonal changes in the actual species constituting these groupings may be obscured. This is a relatively minor problem in offshore regions dominated by identifiable mesopelagic species; it is a much greater problem in inshore regions where groupings (primarily *Sebastes* spp, *Citharichthys* spp, and Sciaenidae) are among the dominant taxa. These groupings have increased apparent similarities between and within the inshore and southern regions.

RESULTS

Total CalCOFI Area Ichthyoplankton Composition

The PL contributed 75.5% of the total larval fish captured in 1975. The most abundant PL species were the northern anchovy (*Engraulis mordax;* 58.9%), Pacific hake (*Merluccius productus;* 14.5%), and jack mackerel (*Trachurus symmetricus;* 2.0%) (Table 1). The OL were dominated by mesopelagic fishes (89 taxonomic categories; 16.7% of the area total). Nine species made up over two-thirds of this fraction and 12.1% of the total larvae. These included one gonostomatid (*Vinciguerria lucetia*), three bathylagids (*Leuroglossus stilbius, Bathylagus wesethi,* and *B. ochotensis*), and five myctophids (*Triphoturus mexicanus, Stenobrachius leucopsarus, Protomyctophum crockeri, Diogenichthys laternatus* and *Tarletonbeania crenularis*). Continental shelf fishes (92 taxa) made up only 7% of the total; flatfishes (Pleuronectiformes; 3.4%), rockfishes (*Sebastes* spp; 3.1%), and croakers (Sciaenidae; 0.5%) predominated.

Geographical Differences in Species Composition

There were large geographical differences in ichthyoplankton composition. Latitudinal and inshore-offshore differences occurred in the relative abundances of the PL, mesopelagic, shelf, and oceanic fractions, and in the species making up these fractions. The greatest difference was the dominance of the PL south of Point Conception (36.1-92.0% regional totals) versus its relatively low abundance off central California (≤5%) (Table 2). This dominance was due primarily to anchovy and hake, and secondarily to jack mackerel, all of which were rare off central California and had greatest abundances off southern Cali-

TABLE 1
Comparison of Relative Abundances of Larval Fishes Taken during 1975 with Those Taken during Annual CalCOFI Surveys 1955-58

	1975		1955		1956		1957		1958	
	% of total	Rank*	% of total	Rank**	% of total	Rank**	% of total	Rank**	% of total	Rank**
Engraulis mordax	58.92	1	39.03	1	33.05	1	29.70	1	45.21	1
Merluccius productus	14.46	2	16.73	2	23.10	2	15.86	2	12.84	2
Sebastes spp	3.12	3	8.17	3	7.14	3	7.39	4	5.27	4
Citharichthys spp	2.79	5	5.68	4	5.79	4	3.20	9	1.46	11
Leuroglossus stilbius	1.46	8	4.21	5	4.56	5	5.98	5	1.07	12
Sardinops sagax	0.13	26	3.93	6	3.80	6	1.99	11	2.51	7
Trachurus symmetricus	2.03	7	3.69	7	1.97	10	4.05	6	1.41	10
Triphoturus mexicanus	2.84	4	3.67	8	2.65	8	3.28	8	3.63	5
Vinciguerria lucetia	2.17	6	3.52	9	2.41	9	11.17	3	12.27	3
Stenobrachius leucopsarus	1.40	9	2.08	10	3.71	7	3.70	7	2.62	6
Diogenichthys laternatus	0.77	13	1.33	11	0.77	13	2.35	10	1.55	8
Bathylagus wesethi	1.05	10	0.90	12	0.52	17	1.29	12	1.54	9
Lampanyctus ritteri	0.40	19	0.55	13	0.47	18	0.56	14	0.68	13
Scomber japonicus	0.005	—	0.54	14	0.37	20	0.38	18	0.28	20
Protomyctophum crockeri	0.78	12	0.51	15	0.45	19	0.29	22	0.39	15
Bathylagus ochotensis	0.98	11	0.36	18	0.55	15	0.22	25	0.34	16
Melamphaes spp	0.24	22	0.22	25	0.26	24	0.27	24	0.28	21
Cyclothone spp	0.63	14	0.43	16	0.20	—	0.58	13	0.62	14
Tarletonbeania crenularis	0.61	15	0.28	21	0.82	12	0.32	21	0.12	—
Argentina sialis	0.05	—	0.23	24	0.32	22	0.28	23	0.06	—
Prionotus spp	0.006	—	—	—	0.60	14	0.55	15	0.29	19
Synodus spp	0.03	—	0.18	—	0.23	25	0.47	17	0.27	23
Pleuronichthys spp	0.06	—	0.29	19	0.27	23	0.12	—	0.04	—
Diaphus theta	0.11	29	0.28	20	0.87	11	0.14	—	0.13	—
Sciaenidae	0.53	16	0.24	23	0.02	—	0.06	—	0.30	18
Symphurus spp	0.05	—	0.02	—	0.34	21	0.32	20	0.05	—
Ceratoscopelus townsendi	0.13	26	0.12	—	0.05	—	0.53	16	0.31	17
Symbolophorus californiense	0.29	20	0.18	—	0.11	—	0.33	19	0.27	22
Icichthys lockingtoni	0.09	30	0.39	17	0.22	—	0.16	—	0.10	—
Peprilus simillimus	0.05	—	0.26	22	0.15	—	0.16	—	0.02	—
Tetragonurus spp	0.03	—	0.14	—	0.53	16	0.14	—	0.01	—
Stomias spp	0.13	26	0.11	—	0.02	—	0.05	—	0.26	24
Hygophum spp	0.03	—	0.11	—	0.05	—	0.16	—	0.22	25
Diogenichthys atlanticus	0.49	17	0.20	—	0.19	—	0.16	—	0.14	—
Other larvae	3.14		1.42		3.41		4.10		3.44	

*Ranks provided for first 30
**Ranks provided for first 25
1955-58 data from Ahlstrom (1965); and Moser and Ahlstrom (1970) based on total numbers of larvae caught (pooled cruises) each year. 1975 data based on summed regional abundances (mean abundances corrected for region area) from six cruises; taxonomic categories adjusted (i.e., species lumped) to conform with earlier data sets.

fornia and northern Baja California (Tables 2, 3). The other PL species (sardine and Pacific mackerel) were caught in a few regions off Baja California and were comparatively rare (< 2% PL in each region).

As expected, both abundances and relative proportions of PL and shelf forms decreased, and those of mesopelagic and oceanic forms increased, with distance from shore. Within the PL, relative proportions of anchovy larvae generally decreased, while those of hake and jack mackerel increased, from inshore to offshore and seaward regions (Table 3).

Within the OL, major contributors to the shelf and mesopelagic categories had marked geographical differences (Table 2). Among the shelf forms, abundances of rockfishes decreased, and flatfishes increased, from north to south; both decreased offshore. Rockfishes dominated the OL of California inshore regions 4 and 7 (41.7-46.7% total OL) and were relatively abundant in northern Baja California region 11 (26.6%); they were relatively rare (≤ 3.9%) in other Baja California regions. Flatfish larvae were most abundant off Baja California in Viscaino Bay

TABLE 2
Percentage Contribution of Major Taxonomic Categories to the Total Ichthyoplankton Collected in Each of 11 CalCOFI Regions and to the Total (Pooled Regions) 1975 CalCOFI Survey Area

Taxonomic Category Area: Region:	Central California		Southern California			Northern Baja California				Central Baja California		
	4 (Inshore)	5 (Offshore)	7 (Inshore)	8 (Offshore)	9 (Seaward)	11 (Inshore)	12 (Bay)	13 (Offshore)	14 (Seaward)	16 (Inshore)	17 (Offshore)	Total
PL	5.01	4.09	82.72	91.94	83.15	91.06	81.49	82.84	36.11	85.47	59.12	75.56
Mesopelagic taxa	42.01	81.05	7.04	5.84	15.12	4.31	2.15	16.49	60.91	6.91	33.80	16.67
Myctophidae	22.42	46.40	2.10	2.55	8.42	2.46	1.57	9.37	25.91	4.85	20.18	8.66
Bathylagidae	18.44	23.60	4.62	2.45	3.45	0.96	0.18	2.30	9.70	0.50	0.89	3.65
Gonostomatidae	0.22	1.37	0.03	0.20	0.98	0.28	0.14	3.00	19.44	1.12	10.83	2.97
Others	0.93	9.68	0.29	0.64	2.27	0.61	0.26	1.82	5.86	0.44	1.90	1.49
Shelf taxa	52.85	14.45	10.23	2.20	1.50	4.60	16.35	0.53	2.77	7.55	7.03	7.58
Rockfishes	44.32	7.41	7.21	1.61	0.57	2.38	0.72	0.09	0.06	0.57	0.36	3.13
Flatfishes	3.71	6.37	0.80	0.34	0.51	0.92	14.39	0.37	2.47	3.95	5.51	3.14
Sciaenids	2.36	—	1.57	0.02	—	0.66	0.50	—	—	0.57	0.65	0.52
Others	2.46	0.67	0.65	0.23	0.42	0.64	0.74	0.07	0.24	2.46	0.51	0.79
Oceanic taxa	0.13	0.41	0.006	0.03	0.23	0.03	0.01	0.14	0.21	0.07	0.05	0.10
Total larval abundance (x 10^{13})	0.68	0.55	3.78	3.16	2.81	2.23	2.64	2.68	1.90	2.40	1.92	24.76

Estimated total abundances derived from summation of mean regional abundances adjusted for region area.

TABLE 3
The 18 Most Abundant Larval Fish Taxa (Including the 10 Most Abundant Species Identifications) in Order of Ranked Abundance, and Their Percentage Contribution to the Total Ichthyoplankton within Each of 11 CalCOFI Regions, 1975

Central California	Region 4 (inshore)			Region 5 (offshore)		
Rank		no/10m²	%		no/10m²	%
1	*Sebastes* spp	441.6	40.2	*Stenobrachius leucopsarus*	97.5	17.5
2	*Stenobrachius leucopsarus*	142.2	12.9	*Bathylagus ochotensis*	87.2	15.6
3	*Leuroglossus stilbius*	93.6	8.5	*Tarletonbeania crenularis*	67.3	12.1
4	*Bathylagus ochotensis*	92.7	8.4	*Sebastes* spp	30.7	5.5
5	*Tarletonbeania crenularis*	74.4	6.8	*Protomyctophum crockeri*	30.5	5.5
6	*Merluccius productus*	34.7	3.2	*Leuroglossus stilbius*	28.1	5.0
7	*Sebastes jordani*	32.7	3.0	*Diaphus* spp	22.8	4.1
8	Sciaenidae	25.9	2.4	*Melamphaes* spp	19.2	3.4
9	*Engraulis mordax*	20.4	1.9	*Citharichthys stigmaeus*	16.5	3.0
10	*Citharichthys stigmaeus*	15.3	1.4	*Citharichthys sordidus*	13.5	2.4
11	*Protomyctophum crockeri*	13.3	1.2	*Merluccius productus*	12.3	2.2
12	*Sebastes paucispinis*	10.9	1.0	*Chauliodus macouni*	10.1	1.8
13	*Bathylagus pacificus*	10.1	0.9	*Sebastes paucispinis*	10.0	1.8
14	*Parophrys vetulus*	8.3	0.8	*Lampanyctus ritteri*	9.5	1.7
15	*Icichthys lockingtoni*	5.8	0.5	*Engraulis mordax*	9.0	1.6
16	*Citharichthys sordidus*	5.7	0.5	*Diogenichthys atlanticus*	7.5	1.3
17	*Citharichthys* spp	5.7	0.5	*Lampanyctus* spp	7.5	1.3
18	*Diaphus theta*	5.5	0.5	*Icichthys lockingtoni*	7.2	1.3
	94.6% of total larvae			87.1% of total larvae		

Ranks based on summed mean abundances (numbers per 10 m² sea-surface area) of each taxon from six cruises within each region

Continued on next page

TABLE 3 (continued)

Southern California

Rank	Region 7 (inshore)	no/10m²	%	Region 8 (offshore)	no/10m²	%
1	*Engraulis mordax*	4333.1	79.5	*Engraulis mordax*	6016.0	78.3
2	*Sebastes* spp	349.7	6.4	*Merluccius productus*	997.7	13.0
3	*Leuroglossus stilbius*	226.3	4.1	*Sebastes* spp	119.9	1.6
4	*Merluccius productus*	177.0	3.2	*Leuroglossus stilbius*	117.3	1.5
5	*Stenobrachius leucopsarus*	87.8	1.6	*Stenobrachius leucopsarus*	59.0	0.8
6	Sciaenidae	81.0	1.5	*Bathylagus ochotensis*	58.8	0.8
7	*Bathylagus ochotensis*	24.7	0.4	*Trachurus symmetricus*	49.3	0.6
8	*Sebastes jordani*	20.5	0.4	*Protomyctophum crockeri*	37.0	0.5
9	*Sebastes paucispinis*	16.8	0.3	*Tarletonbeania crenularis*	28.2	0.4
10	*Citharichthys stigmaeus*	13.1	0.2	*Citharichthys stigmaeus*	17.7	0.2
11	Gobiidae	9.2	0.2	*Lampanyctus ritteri*	15.2	0.2
12	*Argyropelecus* spp	8.8	0.2	*Argyropelecus* spp	14.6	0.2
13	*Citharichthys stigmaeus*	8.0	0.1	*Lampanyctus* spp	14.0	0.2
14	*Tarletonbeania crenularis*	7.8	0.1	*Triphoturus mexicanus*	13.5	0.2
15	*Protomyctophum crockeri*	6.7	0.1	*Bathylagus wesethi*	12.5	0.2
16	*Sebastes levis*	6.0	0.1	*Chauliodus macouni*	12.2	0.2
17	*Parophrys vetulus*	5.6	0.1	*Cyclothone* spp	8.0	0.1
18	*Pleuronichthys verticalis*	5.5	0.1	*Diaphus theta*	6.3	0.1
	98.6% of total larvae			99.1% of total larvae		

Southern California

Rank	Region 9 (seaward)	no/10m²	%
1	*Merluccius productus*	2119.6	74.9
2	*Engraulis mordax*	206.8	7.3
3	*Stenobrachius leucopsarus*	62.3	2.2
4	*Bathylagus ochotensis*	36.7	1.3
5	*Protomyctophum crockeri*	36.6	1.3
6	*Leuroglossus stilbius*	30.7	1.1
7	*Bathylagus wesethi*	27.0	1.0
8	*Trachurus symmetricus*	26.7	0.9
9	*Diogenichthys atlanticus*	23.3	0.8
10	*Tarletonbeania crenularis*	21.3	0.8
11	*Lampanyctus ritteri*	20.5	0.7
12	*Symbolophorus californiense*	17.8	0.6
13	*Sebastes* spp	14.8	0.5
14	*Diaphus* spp	13.2	0.5
15	*Argyropelecus* spp	11.3	0.4
16	*Melamphaes* spp	10.7	0.4
17	*Cyclothone* spp	10.6	0.4
18	*Chauliodus macouni*	10.1	0.4
	95.5% of total larvae		

Northern Baja California

Rank	Region 11 (inshore)	no/10m²	%	Region 12 (inshore-Viscaino Bay)	no/10m²	%
1	*Engraulis mordax*	5749.8	81.8	*Engraulis mordax*	5826.8	80.5
2	*Merluccius productus*	643.2	9.1	*Citharichthys* spp	709.6	9.8
3	*Sebastes* spp	163.8	2.3	*Citharichthys xanthostigma*	194.2	2.7
4	*Triphoturus mexicanus*	88.8	1.3	*Triphoturus mexicanus*	73.0	1.0
5	*Leuroglossus stilbius*	49.7	0.7	*Citharichthys stigmaeus*	55.2	0.8
6	Sciaenidae	44.1	0.6	*Sebastes* spp	45.7	0.6
7	*Citharichthys* spp	30.9	0.4	*Merluccius productus*	39.4	0.5
8	*Protomyctophum crockeri*	27.9	0.4	*Citharichthys sordidus*	35.9	0.5
9	*Lampanyctus ritteri*	20.6	0.3	Sciaenidae	34.7	0.5
10	*Argyropelecus* spp	20.0	0.3	*Sardinops sagax*	32.2	0.4
11	Clinidae	16.5	0.2	*Peprilus simillimus*	20.6	0.3
12	*Trachurus symmetricus*	13.1	0.2	*Paralichthys californicus*	18.6	0.3
13	Gobiidae	11.5	0.2	*Pleuronichthys verticalis*	9.6	0.1
14	*Lampanyctus* spp	10.7	0.2	*Protomyctophum crockeri*	9.3	0.1
15	*Vinciguerria lucetia*	10.1	0.1	*Lampanyctus ritteri*	9.0	0.1
16	*Bathylagus ochotensis*	9.9	0.1	*Leuroglossus stilbius*	8.7	0.1
17	*Citharichthys stigmaeus*	9.0	0.1	*Argentina sialis*	8.2	0.1
18	Cottidae	7.9	0.1	*Diogenichthys atlanticus*	7.7	0.1
	98.4% of total larvae			98.5% of total larvae		

Continued on next page

TABLE 3 (continued)
The 18 Most Abundant Larval Fish Taxa (Including the 10 Most Abundant Species Identifications) in Order of Ranked Abundance, and Their Percentage Contribution to the Total Ichthyoplankton within Each of 11 CalCOFI Regions, 1975

Northern Baja California

Rank	Region 13 (offshore)	no/10m²	%	Region 14 (seaward)	no/10m²	%
1	*Engraulis mordax*	2454.4	65.5	*Trachurus symmetricus*	361.7	19.0
2	*Merluccius productus*	535.8	14.3	*Merluccius productus*	297.9	15.6
3	*Triphoturus mexicanus*	199.6	5.3	*Vinciguerria lucetia*	269.1	14.1
4	*Trachurus symmetricus*	110.6	3.0	*Triphoturus mexicanus*	234.5	12.3
5	*Vinciguerria lucetia*	77.7	2.1	*Bathylagus wesethi*	171.6	9.0
6	*Bathylagus wesethi*	54.8	1.5	*Cyclothone* spp	68.2	3.6
7	*Protomyctophum crockeri*	46.9	1.2	*Diogenichthys atlanticus*	60.0	3.1
8	*Argyropelecus* spp	20.7	0.6	*Protomyctophum crockeri*	47.9	2.5
9	*Diogenichthys atlanticus*	20.6	0.6	*Citharichthys xanthostigma*	38.7	2.0
10	*Lampanyctus ritteri*	19.6	0.5	*Symbolophorus californiense*	34.6	1.8
11	*Cyclothone* spp	16.3	0.4	*Argyropelecus* spp	32.6	1.7
12	*Bathylagus ochotensis*	16.0	0.4	*Lampanyctus ritteri*	31.9	1.7
13	*Symbolophorus californiense*	14.6	0.4	*Engraulis mordax*	28.4	1.5
14	*Lampanyctus* spp	14.1	0.4	*Ceratoscopelus townsendi*	19.4	1.0
15	*Melamphaes* spp	12.7	0.3	*Stomias* spp	15.7	0.8
16	*Leuroglossus stilbius*	11.6	0.3	*Melamphaes* spp	14.8	0.8
17	*Citharichthys stigmaeus*	9.4	0.2	*Diogenichthys laternatus*	13.6	0.7
18	*Ceratoscopelus townsendi*	8.1	0.2	*Lampanyctus* spp	12.3	0.6
	97.2% of total larvae			91.8% of total larvae		

Central Baja California

Rank	Region 16 (inshore)	no/10m²	%	Region 17 (offshore)	no/10m²	%
1	*Engraulis mordax*	4079.9	83.9	*Engraulis mordax*	1439.5	58.3
2	*Triphoturus mexicanus*	166.0	3.4	*Vinciguerria lucetia*	239.0	9.7
3	*Citharichthys* spp	135.0	2.8	*Triphoturus mexicanus*	225.9	9.2
4	*Diogenichthys laternatus*	53.3	1.1	*Diogenichthys laternatus*	187.9	7.6
5	*Vinciguerria lucetia*	43.2	0.9	*Citharichthys* spp	118.0	4.8
6	*Sardinops sagax*	41.6	0.9	*Argyropelecus* spp	26.8	1.1
7	Sciaenidae	27.8	0.6	*Lampanyctus* spp	21.6	0.9
8	*Sebastes* spp	22.1	0.4	*Cyclothone* spp	19.1	0.8
9	*Leuroglossus stilbius*	18.7	0.4	*Ceratoscopelus* spp	16.0	0.6
10	*Sarda chiliensis*	17.5	0.4	Sciaenidae	16.0	0.6
11	*Hypsoblennius* spp	16.1	0.3	*Trachurus symmetricus*	13.4	0.5
12	*Chromis punctipinnis*	15.5	0.3	*Bathylagus wesethi*	12.4	0.5
13	Serranidae	14.9	0.3	*Diogenichthys atlanticus*	9.7	0.4
14	*Etropus* spp	12.8	0.3	*Gonichthys tenuiculus*	9.3	0.4
15	*Citharichthys xanthostigma*	12.5	0.3	*Stomias* spp	9.1	0.4
16	*Merluccius productus*	11.9	0.2	*Sebastes* spp	8.9	0.4
17	*Symphurus* spp	11.2	0.2	*Hippoglossina stomata*	8.9	0.4
18	*Argyropelecus* spp	10.2	0.2	*Bathylagus pacificus*	8.0	0.3
	96.9% of total larvae			96.9% of total larvae		

region 12 (77.8% OL), inshore region 16 (27.7%), and offshore region 17 (13.5%); they were relatively rare (≤ 10% OL) in northern regions. Sciaenid larvae were most abundant (7.4-9.1% OL) in southern California and northern Baja California inshore regions 7 and 11. Among the mesopelagic forms, abundances of Bathylagidae decreased, while those of Myctophidae and Gonostomatidae increased, from north to south and inshore to offshore regions (Table 2). Bathylagid larvae were relatively abundant off central and southern California (19.4-30.4% OL) and rare off Baja California (1.0-15.2%); gonostomatids were rare (0.2-5.8% OL) in all California regions and inshore Baja California regions 11, 12, and 16 but were relatively abundant (17.4-49.4%) in Baja California offshore and seaward regions 13, 14, and 17.

Geographical differences in ichthyoplankton composition were tested using PSI comparisons of total species lists (six cruises combined) from each area and region. We found a high degree of similarity in species percentage composition of the total ichthyoplankton between areas and regions south of Point Conception (Table 4A). High PSI values (ranging from 60.0 to 90.0) resulted from overall comparisons of the southern California and northern and central Baja California areas and from comparisons of the regions

TABLE 4

Percent Similarity Index (PSI) Values for Between-Area and Between-Region Comparisons: (A) Total Ichthyoplankton and (B) Other Larvae (OL)

(A) Total ichthyoplankton PSI values

	Area		
	SC	NBC	CBC
CC	17.97	12.05	6.63
SC		74.29	62.15
NBC			77.08

		Region									
		CC	SC			NBC				CBC	
		5	7	8	9	11	12	13	14	16	17
CC	4	52.15	21.54	12.16	15.53	11.51	6.11	9.01	9.19	4.72	5.27
	5		16.88	11.71	18.50	9.33	4.97	10.68	16.10	3.79	6.29
SC	7			86.92	15.46	88.44	82.68	70.50	6.80	82.40	60.46
	8				27.16	92.13	80.84	82.42	18.72	80.60	61.20
	9					20.82	10.16	30.47	27.95	10.12	12.19
NBC	11						85.11	78.94	14.69	86.48	63.12
	12							68.71	6.53	87.96	66.33
	13								34.99	71.96	70.33
	14									8.84	27.56
CBC	16										69.31

(B) Other larvae PSI values

	Area		
	SC	NBC	CBC
CC	69.02	20.69	10.22
SC		34.88	19.45
NBC			62.28

		Region									
		CC	SC			NCB				CBC	
		5	7	8	9	11	12	13	14	16	17
CC	4	50.76	70.36	59.44	43.05	47.81	11.73	10.69	5.62	11.58	6.36
	5		29.26	57.44	62.54	29.17	13.46	23.98	16.25	9.94	8.02
SC	7			56.97	28.56	55.54	14.79	9.68	6.02	17.15	7.60
	8				62.78	53.30	14.80	31.57	23.14	15.78	14.86
	9					37.40	13.08	46.40	37.94	16.13	16.85
NBC	11						27.33	42.17	36.16	39.45	34.20
	12							14.10	14.71	42.19	25.12
	13								69.71	40.13	49.53
	14									36.34	55.67
CBC	16										58.66

Based on pooled (6 cruises) species lists for each area and region, 1975. CC = central California; SC = southern California; NBC = northern Baja California; CBC = central Baja California.

within each of these areas (Table 4A). Low PSI values (< 25) resulted from comparisons of the total species lists of regions and areas north and south of Point Conception and reflect the dominance of the PL species south of Point Conception. When PL species were excluded and comparisons were made between the relative proportions of the OL, high PSI values (62.3-69.0) were found for comparisons between the central and southern California areas and between the northern and central Baja California areas; low PSI values (10.2-34.9) were found for comparisons between the California and Baja California areas (Table 4B). Aside from dominance by the PL, the species proportions of the southern California ichthyoplankton were dissimilar to those of the northern and central Baja California areas, but were fairly similar to those of central California. Highest between-region OL PSI values occurred between inshore regions 4-7 (70.4) and offshore and seaward regions 5-9 (62.5) and 8-9 (62.8) of central and southern California and between offshore and seaward regions 13-14 (69.7) of northern Baja California (Table 4B). These high PSI values reflect similarities in proportions of the dominant shelf and mesopelagic taxa (Table 3) in these regions.

Geographical differences in taxonomic composition and relative abundance were tested using Kendall's tau test comparisons of the rank order of abundances of the 10 most abundant taxa (six cruises pooled) within each area and region (Table 3). All comparisons that included the PL in the rankings supported ($P > 0.10$) the null hypothesis of no agreement of species rank order of abundance. When the PL were excluded, significant agreement ($P < 0.05$) of rank order of abundance among the 10 most abundant OL taxa occurred between regions 4-7, 4-8, 5-8, and 5-9 off central and southern California and between regions 13-14 off northern Baja California.

Seasonal Differences in Ichthyoplankton Species Structure

The ichthyoplankton underwent large seasonal abundance fluctuations because of seasonal spawning of the main PL species (Figure 1). Maximum areawide abundances of anchovy, hake, and jack mackerel occurred in January and March, during which time the the PL made up 84% of the total larvae (TL). PL also dominated the ichthyoplankton during May (67% TL). Shelf forms were most abundant during January and March because of peak abundances of rockfish larvae, but because of PL dominance they made up only 4% (rockfishes 3%) of the total. Sciaenids had a January abundance peak (0.5% TL). Lower, relatively constant numbers of shelf forms occurred from May to October-November, and flatfishes predominated (8-

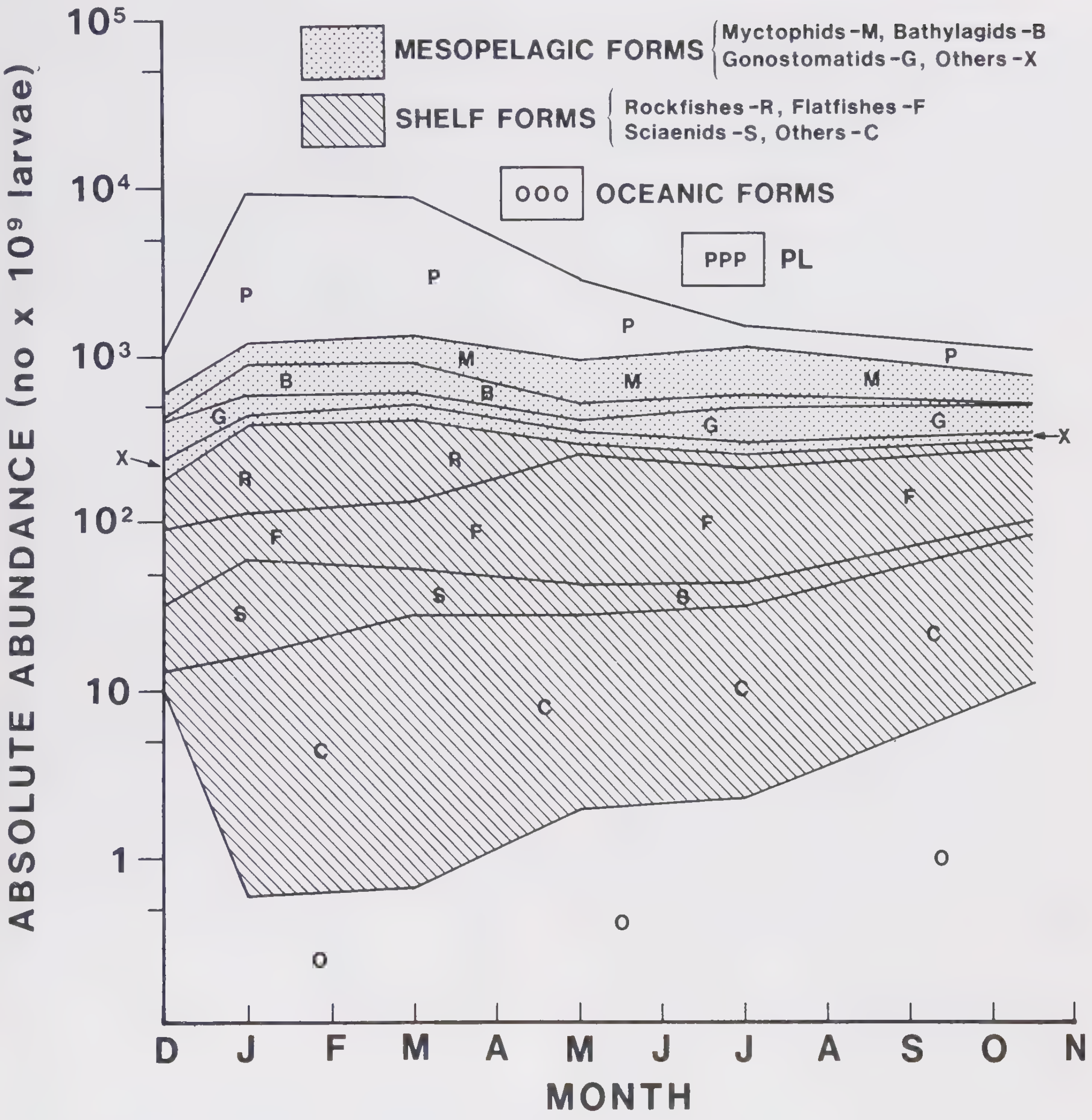

Figure 1 Seasonal abundance fluctuations of major ichthyoplankton categories in the CalCOFI area (all regions combined) during 1975. Categories include PL (anchovy, hake, jack mackerel, sardine, Pacific mackerel); mesopelagic forms (myctophids, bathylagids, gonostomatids, others), shelf forms (rockfishes, flatfishes, sciaenids, others); and oceanic forms. Abundances expressed as estimated absolute numbers · 10^9 of larvae in the survey area during each cruise. Log scale is used to depict simultaneous abundance fluctuations of forms representing a wide range of relative abundances

16% TL). Other shelf taxa were most abundant during October (7% TL). Mesopelagic forms had two abundance peaks caused by increased spawning of myctophids and bathylagids during January and March, and of myctophids and gonostomatids during July. Because of decreased PL abundances, mesopelagic species dominated the ichthyoplankton in July and October-November (57% and 40% TL), and were about equal to the PL in December (mesopelagics 39%; PL 43%). Oceanic species were most abundant (1% TL) during October-November and December.

Each region had seasonal changes in abundance and relative proportions of major taxa (Figures 2, 3) and species. Maximum PL abundances within all regions occurred between January and May because of peak spawning of anchovy, hake, and jack mackerel; these larvae dominated the ichthyoplankton of all regions south of Point Conception for part or all of this period. Dominance was greatest in inshore regions where the PL made up 80-96% of the total larvae caught from January to May (and July in southern California region 7). PL dominance in offshore regions was restricted to January and March in southern California regions 8 and 9 and northern Baja California region 13 (84-97% TL), and to March in northern and central Baja California regions 14 and 17 (72-84% TL). Seasonal abundance fluctuations of the PL are treated in greater detail in Loeb et al. (1983a).

Seasonal and regional patterns of OL composition and abundance relations were complex. However, four general patterns can be established based on regional similarities of overall dominant taxa. These occur between (1) inshore central and southern California and northern Baja California regions 4, 7, and 11; (2) offshore central and southern California regions 5, 8, and 9; (3) Viscaino Bay and central Baja California inshore regions 12 and 16; and (4) offshore Baja California regions 13, 14, and 17 (Figures 2, 3).

California and northern Baja California inshore regions 4, 7, and 11. OL abundances in the California and northern Baja California inshore regions were elevated from December to March and then (except in region 7 during October) decreased to low and relatively constant levels for the rest of the year. Maximum spring abundances occurred during January and March and were due to large numbers of rockfish, bathylagid, and myctophid larvae (64.6-94.7% OL within each region). Major contributing taxa were *Sebastes* spp, the bathylagids *Leuroglossus stilbius* and *Bathylagus ochotensis*, and myctophids *Stenobrachius leucopsarus* (regions 4 and 7) and *Protomyctophum crockeri* (regions 7 and 11). Abundances of all major categories (except myctophids in region 11) decreased in May and, except for flatfishes, remained low for the rest of the year. In region 11 myctophids had a July abundance maximum dominated by *Triphoturus mexicanus*. Large regional differences occurred in the composition and proportions of major taxa from May to November. Flatfish abundance peaks occurred during October-November in all three regions and were primarily due to large numbers of *Citharichthys* spp, *C. stigmaeus*, *C. sordidus*, and (in region 4) *Parophrys vetulus*. Flatfish abundance was most extreme in region 7 during October, when maximum OL abundance (81% because of flatfishes) occurred. Flatfishes made up 25.5% of the October OL in region 11 and 19.6% and 34.6% of the November OL in regions 4 and 7, respectively.

Central and southern California offshore and seaward regions 5, 8, and 9. OL abundances in California offshore and seaward regions were elevated during January and March (and May in regions 5 and 9) primarily because of peak spawning of myctophids and bathylagids. Five species—*Leuroglossus stilbius* and *Bathylagus ochotensis* (Bathylagidae) and *Stenobrachius leucopsarus*, *Protomyctophum crockeri*, and *Tarletonbeania crenularis* (Myctophidae)—were consistently abundant and made up 37.8%-70.5% of the OL in each region during this period. Rockfish larvae were also abundant during January and March in regions 5 and 8 (9.0-26.8% OL) and during May in region 9 (6.3%). OL abundances in all three regions decreased from May to October-November, and species composition and relative proportions varied with region and cruise. Flatfishes (*Citharichthys* spp, *C. stigmaeus*, and *C. sordidus*) were most abundant during November (region 8, 24.0%) and December (regions 5 and 9, 25.6% and 12.2% OL, respectively). Oceanic forms were most abundant in region 8 during December (2.3% OL) and in region 9 during November and December (3.6-4.0%).

Viscaino Bay and central Baja California inshore regions 12 and 16. Flatfishes dominated region 12 OL throughout the year (51.6-83.9% within each cruise). Flatfishes dominated region 16 OL during December (48.5%) and were major contributors (31.9-43.0%) during May and October; myctophids dominated during January, May, and July (40.3-52.7%); other shelf forms dominated in October (39.8%). In contrast to the northern inshore regions, January and March OL abundances were relatively low; maximum numbers of rockfishes, bathylagids (primarily *Leuroglossus stilbius*), and sciaenids (in region 12) occurred during this time. Greatest OL abundances occurred during May and July in region 12, and July and October in region 16 because of maximum numbers of flatfishes (primarily *Citharichthys* spp, *C. xanthostigma*, *C. sordidus*, *C. stigmaeus*, *Paralichthys californicus*, and *Symphurus* sp); myctophids (primarily *Triphoturus mexicanus* in region 12, *T. mexicanus* and *Diogenichthys laternatus* in region 16); gonostomatids (in region 16, *Vinciguerria lucetia*); sciaenids (region 16); and other shelf taxa (*Peprilus simillimus* in region 12, *Chromis punctipinnis*, Serranidae, *Etropus* sp, and *Chloroscombrus* sp in region 16). The peak July OL abundances in Viscaino Bay were the highest for the entire CalCOFI area during 1975; the July and October abundances of other shelf taxa in region 16 were greater than in any other region during the year.

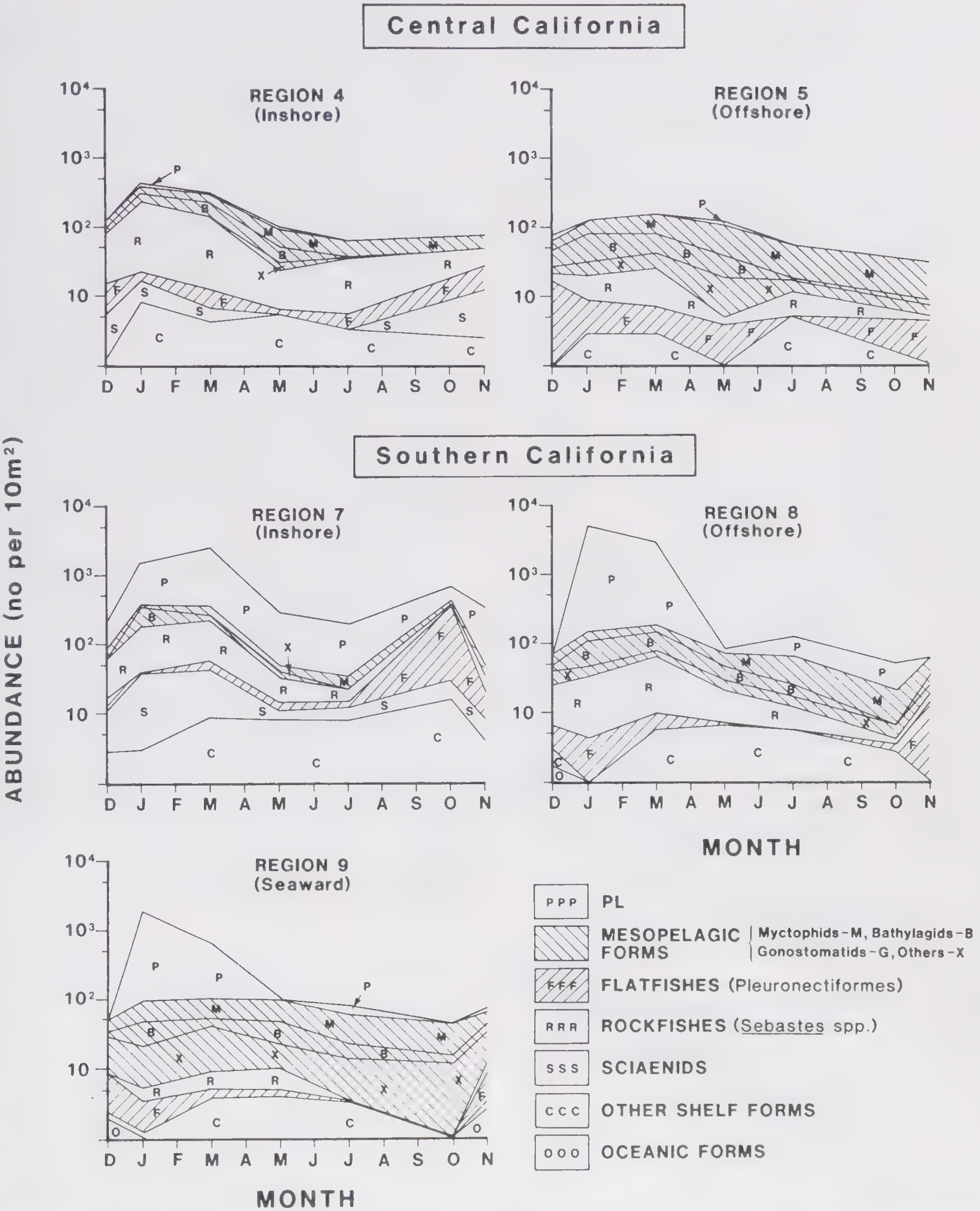

Figure 2. Seasonal abundance fluctuations of major ichthyoplankton categories within CalCOFI regions 4, 5, 7, 8, and 9 during 1975. Categories include PL (anchovy, hake, jack mackerel, sardine, Pacific mackerel); mesopelagic forms (myctophids, bathylagids, gonostomatids, others); shelf forms (rockfishes, flatfishes sciaenids, others); and oceanic forms. Abundances are expressed as mean numbers of larvae per 10 m^2 sea-surface area during each cruise. Log scale is used to depict simultaneous fluctuations of forms representing a wide range of relative abundances.

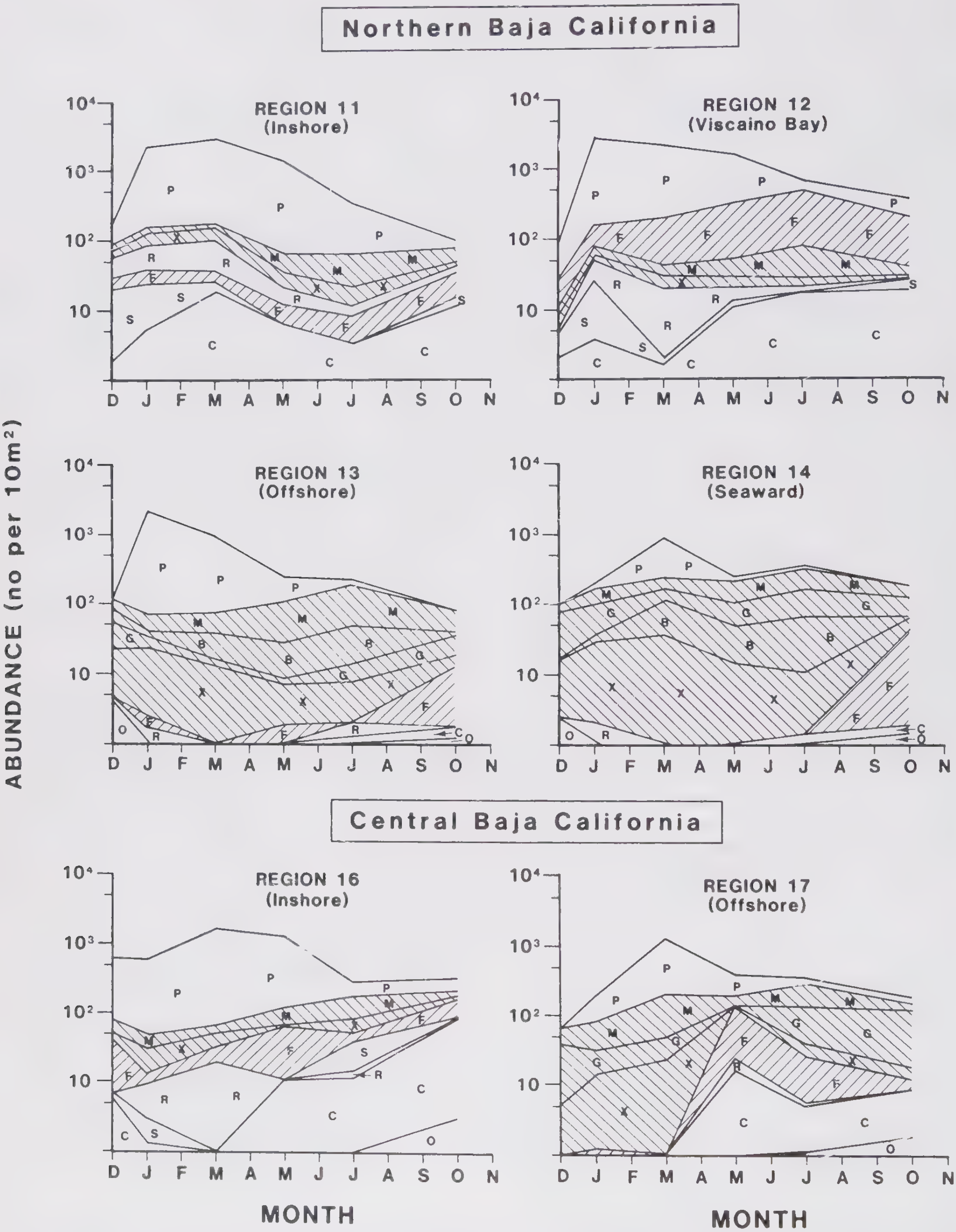

Figure 3. Seasonal abundance fluctuations of major ichthyoplankton categories within CalCOFI regions 11-14, 16, and 17 during 1975. Categories include PL (anchovy, hake, jack mackerel, sardine, Pacific mackerel); mesopelagic forms (myctophids, bathylagids, gonostomatids, others); shelf forms (rockfishes, flatfishes, sciaenids, others), and oceanic forms. Abundances are expressed as mean numbers of larvae per 10 m^2 sea-surface area during each cruise. Log scale is used to depict simultaneous fluctuations of forms representing a wide range of relative abundances

Northern central Baja California offshore and seaward regions 13, 14, and 17. OL abundances in the Baja California offshore and seaward regions increased from relatively low December-January values to July maxima because of peak abundances of myctophids (mostly *Triphoturus mexicanus*: 38.0-62.9% OL) and, in regions 14 and 17, high gonostomatid abundances (21.4-27.0%; primarily *Vinciguerria lucetia*). Bathylagids (primarily *Bathylagus wesethi*) were most abundant in regions 13 and 14 from March to July (13.0-32.4%); flatfishes were rare or absent in these two regions except during October (13.9% region 13 OL, primarily *Citharichthys stigmaeus* and *C. sordidus;* 26.0% region 14 OL, primarily *C. xanthostigma* and *Symphurus* sp). Because region 17 was undersampled during March and May (5 samples total) little can be determined about the OL during that time. Flatfishes, rockfishes, and sciaenids were abundant in the one May sample; relatively large numbers of flatfishes (6.7% OL, primarily *Citharichthys* spp) were also collected during July. Oceanic forms were most abundant in regions 13 and 14 during December (2.1-3.3%) and in region 17 during October (1.2%).

Within- and Between-Region Comparisons of Ichthyoplankton Species Structure

Seasonal changes in ichthyoplankton composition and abundance relations are reflected by PSI values resulting from between-cruise comparisons of species lists. PSI values from comparisons of the total ichthyoplankton and of the OL fraction (all regions combined) were highest (91 and 73, respectively) for January and March cruise comparisons, and lowest (30-41) for January and March vs July and October-November comparisons. These indicate a marked shift in relative proportions of both PL and OL species between spring and summer/fall. These changes were primarily due to decreased abundances of the main PL species (anchovy, hake, and jack mackerel), rockfishes *(Sebastes spp), Leuroglossus stilbius* and *Bathylagus ochotensis* (Bathylagidae), and *Stenobrachius leucopsarus* (Myctophidae), and increased abundances of *Triphoturus mexicanus* (Myctophidae), *Vinciguerria lucetia* (Gonostomatidae), and flatfishes (primarily *Citharichthys* spp) during July and October-November. Kendall's concordance test of the rank order of abundance of the 10 most abundant species taken during each cruise showed significant agreement ($P < 0.01$) of rank order of abundance throughout the year. This indicates that despite marked seasonal changes in relative proportions, the same abundant taxa tended to dominate the ichthyoplankton throughout the year.

Within each region, marked seasonal shifts in relative proportions of larval fish species are reflected by low between-cruise PSI values (Table 5). The ranges of between-cruise PSI values were smallest in central California regions 4 and 5 (which had little seasonal input of PL) and southern California inshore region 7 (which was dominated by anchovy larvae during all cruises). The other eight regions had large proportions of their total ichthyoplankton contributed by one or more of the PL species during at least two cruises during the year. Because of more equitable abundances among the OL, OL PSI values (except in regions 4, 5, and 14) were lower, and varied less than those for the total ichthyoplankton (Table 5). High (≥ 60) total ichthyoplankton PSI values were associated with periods of maximum PL abundance in all regions except 4 and 5 (central California) and 13 and 14 (northern Baja California); in these four regions, highest values were associated with periods of peak OL abundances. Maximum OL PSI values were also generally associated with periods of peak OL abundances; exceptions were in central Baja California regions 16 and 17, where maximum January-March PSI values preceded July peak OL abundance, and in northern Baja California region 11, where maximum May-July PSI values followed January-March peak abundances.

TABLE 5

Range and Mean of Percent Similarity Index (PSI) Values from Between-Cruise Comparisons of the Total Ichthyoplankton and of the Other Larval Fraction (OL) in 11 CalCOFI Regions, 1975

		Total ichthyoplankton		Other larvae	
	Region	Range	Mean	Range	Mean
Central California					
	4	31.81-70.50	51.62	33.50-74.46	52.06
	5	26.25-59.40	40.61	27.54-64.00	46.68
Southern California					
	7	69.17-93.84	83.12	41.23-72.46	56.57
	8	1.80-85.16	23.51	20.75-75.89	43.69
	9	4.07-87.06	25.88	29.47-67.98	42.64
Northern Baja California					
	11	28.32-93.52	58.97	27.14-68.90	43.91
	12	29.54-93.38	59.81	26.47-82.66	51.88
	13	2.36-50.68	23.87	21.22-73.16	37.44
	14	15.52-86.73	39.76	26.70-86.20	48.06
Central Baja California					
	16	31.26-93.57	54.40	23.90-60.33	37.33
	17	13.93-70.94	40.89	30.57-61.89	48.47

Comparisons based on species lists from each of 6 cruises.

As with area-wide comparisons, low total and OL regional PSI values generally resulted from comparisons of October-November species lists with those of other months. This indicates that, within all regions, the species composition and abundance relations dur-

TABLE 6

Percent Similarity Index (PSI) Values from Between-Region Comparisons of the Other Larvae (OL) Category of Ichthyoplankton Taken in CalCOFI Cruises, 1975

Areas	Regions	Cruise					
		7412	7501	7503	7505	7507	7510(11)
CC-CC	4-5	36.77	40.92	56.73	53.11	56.19	46.21
CC-SC	4-7	67.20*	62.63*	70.45*	47.53	41.76	57.92
CC-SC	4-8	48.54	53.64	66.51*	63.88*	44.47	29.26
CC-SC	4-9	22.27	40.83	51.76	49.00	31.26	20.44
CC-SC	5-7	25.04	26.56	34.18	25.46	31.68	25.23
CC-SC	5-8	40.56	42.61	50.66	58.13	51.40	45.31
CC-SC	5-9	28.72	57.47	71.12*	61.16*	47.31	26.80
SC-SC	7-8	53.04	66.14*	56.73	42.71	34.04	38.01
SC-SC	7-9	17.83	29.54	34.84	33.39	25.15	24.43
SC-SC	8-9	49.25	54.34	50.04	55.32	66.19*	50.36
SC-NBC	7-11	50.91	57.59	67.71*	41.79	28.37	49.92
SC-NBC	7-12	26.28	26.80	17.29	13.83	11.26	42.98
SC-NBC	7-13	7.24	9.87	8.96	15.18	18.08	50.36
SC-NBC	7-14	6.84	4.72	10.24	9.47	13.13	41.52
SC-NBC	8-11	47.85	46.86	53.73	28.21	31.63	41.52
SC-NBC	8-12	16.46	20.25	14.63	4.82	10.77	29.76
SC-NBC	8-13	27.15	24.29	20.83	18.01	33.96	41.18
SC-NBC	8-14	29.47	15.59	20.17	10.67	26.56	24.86
SC-NBC	9-11	28.11	42.58	34.42	23.74	30.71	33.57
SC-NBC	9-12	14.12	45.71	11.78	6.98	11.49	15.04
SC-NBC	9-13	37.64	13.76	33.67	33.90	34.43	51.51
SC-NBC	9-14	41.24	33.94	33.87	27.85	30.27	33.22
NBC-NBC	11-12	32.43	41.26	22.21	17.74	18.89	35.25
NBC-NBC	11-13	26.15	34.54	27.58	57.80	65.81*	43.32
NBC-NBC	11-14	21.07	30.47	23.68	45.26	48.46	29.06
NBC-NBC	12-13	9.93	17.09	11.48	10.22	12.23	21.38
NBC-NBC	12-14	9.39	14.67	7.50	9.54	12.42	28.08
NBC-NBC	13-14	68.31*	46.26	53.85	63.89*	63.60*	57.78
NBC-CBC	11-16	27.14	44.36	44.21	40.99	51.33	35.23
NBC-CBC	11-17	21.02	17.69	13.23	24.93	48.23	17.84
NBC-CBC	12-16	60.97*	38.59	35.82	47.57	20.95	36.99
NBC-CBC	12-17	14.74	10.20	6.45	60.97*	17.41	9.03
NBC-CBC	13-16	13.15	28.80	18.77	38.47	51.85	27.39
NBC-CBC	13-17	59.32	24.72	24.70	16.42	50.58	32.71
NBC-CBC	14-16	11.27	26.37	12.42	40.79	55.55	33.78
NBC-CBC	14-17	53.55	45.69	24.64	16.20	67.45*	48.03
CBC-CBC	16-17	35.18	49.72	26.09	65.70*	67.68*	27.20

Comparisons are between regions of the same area and between regions of adjacent areas.
Asterisk denotes high values (i.e., ⩾60).
CC = central California; SC = southern California; NBC = northern Baja California; CBC = central Baja California.

ing fall were markedly different from those during the rest of the year.

Geographical and seasonal differences in taxonomic composition are shown by within-cruise PSI comparisons between the OL of adjacent regions (Table 6). Most of the PSIs were low (< 40), indicating a great degree of geographical heterogeneity throughout the year. High PSI values were generally associated with comparisons between north-south adjacent regions for the central and southern California areas and with comparisons between inshore-offshore adjacent regions within the northern and central Baja California areas. High between-region similarities were seasonally restricted. Highest PSI values in the California and northern Baja California inshore regions (62.6-70.4) occurred between regions 4-7 during December, January, and March and between regions 7-11 during March. Highest inshore-offshore and offshore-seaward values off California occurred between regions 4-8 and 5-9 during March and May, regions 7-8 in January, and regions 8-9 in July. Except for the last, these high PSI values reflect similar proportions of dominant rockfish, bathylagid, and myctophid species (*Sebastes* spp, *Leuroglossus stilbius, Bathylagus ochotensis, Stenobrachius leucopsarus, Tarletonbeania crenularis, and Protomyctophum crockeri*) during periods of elevated and peak OL abundances. High July values between regions 8-9 reflect similar proportions of a variety of myctophid and bathylagid species during a time of relatively low OL abundance. High PSI values in the Baja California areas (63.9-68.3) occurred between offshore and seaward regions 13-14 during December, May, and July because of similar proportions of dominant myctophid, gonostomatid, and bathylagid species (primarily *Triphoturus mexicanus*, *Vinciguerria lucetia*, and *Bathylagus wesethi*); high values also occurred between regions 11-13, 14-17, and 16-17 during July, and reflect shared dominance by *T. mexicanus* and (in all but region 11) *V. lucetia* during peak OL abundance.

DISCUSSION

Total Ichthyoplankton, 1975

Despite the large interannual variability in flow and biology of the California Current system (Reid et al. 1958; Sette and Isaacs 1960; Colebrook 1977; Bernal 1980), the 1975 ichthyoplankton resembled that taken on CalCOFI cruises between 1955 and 1958 (Table 1). Ahlstrom (1965) found that 12 kinds of larvae consistently contributed between 90% and 93% of the total CalCOFI ichthyoplankton. Eleven of the 12 are among the 13 most abundant taxa taken during 1975 (species were lumped into higher taxonomic categories in 1975 data to conform to the 1955-58 data; Table 1). The one major exception was the sardine (adjusted rank 26 during 1975 vs rank 6-11 in 1955-58).

The 12 most abundant taxa taken during 1975 included 91% of the total ichthyoplankton. The rank order of abundance within these 12 taxa was quite similar to that of 1955-58 (Kendall's tau tests, $P < 0.01$). However, while the proportion of hake larvae (14.5% of the total ichthyoplankton) in 1975 was similar to 1955-58 values, the proportion of anchovy larvae (58.9%) was 1.3 to 2 times higher, and the proportions of the other 10 taxa were reduced (and more similar to each other) in 1975 as compared to 1955-58 (Table 1). Caution must be used in making such direct rank and proportion comparisons between the two sets of data (especially between the less abundant taxa) because the 1955-58 values are based on actual total numbers of larvae caught and not on abundances adjusted for the area sampled (used here). Also, because the 1955-58 data were not standardized, direct comparisons of numerical abundances between 1975 and the earlier years cannot yet be made.

The large-scale CalCOFI sampling plan covers the spawning areas of the major pelagic fishes (sardine, anchovy, hake, jack mackerel) off California and Baja California (Ahlstrom 1965), and the sampled ichthyoplankton is dominated by these abundant and fecund species and by other offshore (mesopelagic) species. Shelf species other than *Sebastes* spp and *Citharichthys* spp (which have long larval periods) make limited contributions.

Geographical differences in larval fish species distributions within the CalCOFI area are to some extent obscured by the widespread distributions of anchovy, hake, and jack mackerel. However, there are distinct underlying patterns of distribution among the other larvae. Some of these species are associated with major Pacific Ocean water masses, or with cold-water (northern) or warm-water (southern) conditions, and year-to-year variations in these species' distributions and abundances have been related to changes in flow within the California Current system (Ahlstrom 1965, 1969; Paxton 1967; Moser and Ahlstrom 1970; Moser et al. 1977). Regional mean abundances of the dominant OL species during 1975 reflected their documented water-mass affiliations (Table 7). Two of three subarctic-transition zone myctophids (*Stenobrachius leucopsarus* and *Tarletonbeania crenularis;* Paxton 1967) and the two "northern" *Sebastes* species (*S. paucipinis* and *S. jordani;* Moser et al. 1977) occurred in greatest abundance off central and southern California. The warm-water cosmopolite *Diogenichthys atlanticus* (Ahlstrom 1965) was most abundant off northern Baja California, and the restricted California Current species (*Protomyctophum crockeri;* Ahlstrom 1965) and eastern tropical Pacific species (*Triphoturus mexicanus*, *Vinciguerria lucetia*, and *Diogenichthys laternatus;* Ahlstrom 1965; Paxton 1967) were most numerous off of northern and central Baja California.

Within the central and southern California areas, maximum abundances of mesopelagic species occurred in inshore region 4, while offshore and seaward regions 8 and 9 were locations of maximum anchovy (region 8) and hake (region 9) abundances (Table 7). In contrast, within the northern and central Baja California areas, mesopelagic species were most abundant in seaward region 14, while inshore regions 11 and 12 had maximum anchovy (region 12) and hake (region 11) abundances (Table 7). These shifts suggest inshore-offshore differences in adult distributions and spawning activities and possible differences in net larval transport between the areas off California and Baja California.

The northern Baja California area was one of faunal transition with marked north-south shifts in regional dominance by rockfishes and bathylagids to dominance by gonostomatids, flatfishes, and other shelf taxa. It also marked shifts in dominance by subarctic, cold-water, and northern species to eastern tropical

TABLE 7

Regional Ranks of Abundance of the 22 Most Abundant Larval Fish Species in the CalCOFI Area, 1975

	Affiliation	Central California		Southern California			Northern Baja California				Central Baja California	
		Region										
		4	5	7	8	9	11	12	13	14	16	17
Stenobrachius leucopsarus	S-T	1	2	3	5	4	7	—	—	6	8	—
Bathylagus ochotensis	N	1	2	5	3	4	7	9	6	8	—	—
Tarletonbeania crenularis	S-T	1	2	5	3	4	7	—	—	6	—	—
Sebastes jordani	N	1	5	2	3	6	4	—	—	—	—	—
Sebastes paucispinis	N	2	3	1	6	5	4	—	—	—	—	—
Leuroglossus stilbius	M	3	6	1	2	5	4	9	8	10	7	11
Engraulis mordax	M	10	11	4	1	8	3	2	6	9	5	7
Merluccius productus	M	8	9	6	2	1	3	7	4	5	10	11
Citharichthys sordidus	N	4	2	10	6	7	5	1	8	—	3	9
Citharichthys stigmaeus	N	4	3	7	2	8	6	1	5	10	9	11
Symbolophorus californiense	T	—	6	10	5	2	4	7	3	1	9	8
Diogenichthys atlanticus	C	11	5	10	8	2	7	6	3	1	9	4
Lampanyctus ritteri	S-T	9	6	10	5	3	2	7	4	1	11	8
Protomyctophum crockeri	CA	7	5	9	3	4	6	8	2	1	11	10
Trachurus symmetricus	M	—	9	10	3	4	6	8	2	1	7	5
Ceratoscopelus townsendi	CA	—	8	9	4	3	7	10	2	1	5	6
Bathylagus wesethi	S	—	9	10	4	3	7	8	2	1	6	5
Citharichthys xanthostigma	S	—	—	—	—	—	—	1	5	2	3	4
Sardinops sagax	M	—	—	4	—	—	3	1	—	2	—	—
Triphoturus mexicanus	ETP	—	—	9	7	8	5	6	3	1	4	2
Vinciguerria lucetia	ETP	—	9	—	8	7	5	6	3	1	4	2
Diogenichthys laternatus	ETP	—	—	7	—	—	6	4	5	3	2	1

Ranks based on total mean numbers of larvae (6 cruises, summed) in each region. Water mass or habitat affiliations assigned to each species: S-T, subarctic-transition zone; T, transition zone; C, warm-water cosmopolite; ETP, eastern tropical Pacific; N, northern/cold water; S, southern/warm water; CA, restricted to California Current; M, multiple affiliations. Affiliations from Ahlstrom (1965), Paxton (1967), Moser and Ahlstrom (1970), and Moser et al. (1977).

Pacific, warm-water, and southern species. Offshore and seaward regions 13 and 14 contained mixtures of species from all three water-mass source areas plus restricted California Current species; dominant OL of inshore regions 11 and 12 included subarctic and eastern tropical Pacific species. The transitional nature of the northern Baja California area is reflected by the relatively low OL PSI values resulting from comparisons of its regions with north-south adjacent regions (Table 4B). Despite its transitional nature, the northern Baja California area had relatively large numbers of larval fishes (Loeb et al. 1983a): PL abundance was extremely high in inshore regions 11 and 12, and maximum areawide OL abundances occurred in regions 12 (primarily flatfishes) and 14 (mesopelagic taxa).

Seasonal changes were evident in both larval fish abundance (Loeb et al. 1983a) and relative abundance of species. However, within each region there was a general dominance by a limited suite of taxa throughout the year. Seasonal differences were probably due to differences in the timing of peak spawning activity among these few abundant taxa. Highest area-wide abundances occurred during the peak January-May PL spawning period. Highest OL abundances occurred during January and March in the central and southern California areas and in inshore region 11 of northern Baja California; this was primarily due to peak spawning of *Sebastes* spp and four mesopelagic species with subarctic-transition zone, northern/cold-water, or restricted affiliations (*Stenobrachius leucopsarus, Protomyctophum crockeri, Leuroglossus stilbius,* and *Bathylagus ochotensis;* Table 8). Low OL abundances prevailed within all of these regions (except region 7) from May to December because of minor sumer/fall spawning input; within region 7, the October OL abundance peak was attributed to *Citharichthys* spp. Within the central Baja California regions and regions 12, 13, and 14 of northern Baja California, maximum OL abundances occurred between May and October primarily because of peak summer or fall spawning of flatfish and southern shelf species and three eastern tropical Pacific or warm-water mesopelagic species (*Triphoturus mexicanus, Vinciguerria lucetia,* and *Bathylagus wesethi;* Table 8).

Ichthyoplankton Distribution and Seasonal Abundance Patterns in Relation to California Current Flow

The dominant OL taxa of the central and southern California areas are subarctic-transition zone, northern, and cold-water forms, and reflect the northern sources of the California Current. These species,

TABLE 8

Cruise Ranks of Abundance of the 22 Most Abundant Larval Fish Species in the CalCOFI Area, 1975

	Affil-iation	Cruise					
		7412	7501	7503	7505	7507	7510(11)
Stenobrachius leucopsarus	S-T	4	2	1	3	5	6
Bathylagus ochotensis	N	4	1	2	3	5	6
Tarletonbeania crenularis	S-T	6	5	4	2	3	1
Sebastes jordani	N	—	—	1	—	—	—
Sebastes paucispinis	N	3	1	2	4	—	5
Leuroglossus stilbius	M	3	1	2	4	5	6
Engraulis mordax	M	4	1	2	3	6	5
Merluccius productus	M	4	1	2	3	5	6
Citharichthys sordidus	N	2	3	5	6	4	1
Citharichthys stigmaeus	N	2	4	3	6	5	1
Symbolophorus californiense	T	6	3	1	4	2	5
Diogenichthys atlanticus	C	3	2	1	5	6	4
Lampanyctus ritteri	S-T	5	1	2	4	3	6
Protomyctophum crockeri	CA	3	1	2	4	5	6
Trachurus symmetricus	M	—	5	1	3	2	4
Ceratoscopelus townsendi	CA	5	4	3	6	2	1
Bathylagus wesethi	S	6	5	1	3	2	4
Citharichthys xanthostigma	S	—	—	—	3	2	1
Sardinops sagax	M	4	3	6	5	1	2
Triphoturus mexicanus	ETP	6	5	4	2	1	3
Vinciguerria lucetia	ETP	3	4	6	5	1	2
Diogenichthys laternatus	ETP	4	3	1	6	2	5

Ranks based on summed adjusted abundances of larvae from 11 CalCOFI regions for each cruise. Water mass or habitat affiliations assigned to each species: S-T, subarctic-transition zone; T, transition zone; C, warm-water cosmopolite; ETP, eastern tropical Pacific; N, northern/cold water; S, southern/warm water; CA, restricted to California Current; M, multiple affiliations. Affiliations from Ahlstrom (1965), Paxton (1967), Moser and Ahlstrom (1970), and Moser et al. (1977).

although present and generally dominant throughout the year, were most abundant in January-March, during reduced surface countercurrent flow and the onset of upwelling. During 1975 the upwelling period in the central and southern California areas extended from March to late September; maximum intensities occurred from May to July (Parrish et al. 1981). Decreased and relatively constant OL abundances prevailed here during most of this upwelling period and throughout most of the surface countercurrent period. The OL species proportions of the inshore regions of the central and southern California areas and inshore region 11 of northern Baja California were most similar from December or January to March (Table 6), possibly because these regions experienced similar environmental conditions at the onset of increased spawning activity by shared dominant taxa. Except for regions 7 and 8, greatest similarity of species proportions between inshore-offshore regions occurred later (March to May or July) than for the inshore regions; this corresponds to the period of maximum offshore advection of surface water associated with upwelling (Bakun and Nelson 1977) and may implicate larval drift. Regions 7 and 8 were most similar during December, January, and March (Table 6), perhaps because of similar wintertime conditions prevailing within the Los Angeles bight area (Lasker 1978). Between-region PSI values were relatively low during summer and fall, suggesting greater environmental heterogeneity (on regional scales) during the period of surface countercurrent flow and reduced upwelling.

The dominant OL taxa of the central Baja California area, and to a lesser degree of the northern Baja California area, are eastern tropical Pacific, southern, and warm-water forms. In these southern regions (except region 11) highest OL abundances occurred during summer and fall. This is a period of decreased upwelling, weakened southward flow, increased surface temperatures, and surface countercurrent flow off Baja California. Throughout the year 67% of all between-region PSI values in these areas were < 40.0 as compared to the regions of central and southern California, where only 33% of all comparisons were < 40.0 (Table 6). This suggests a greater degree of between-region heterogeneity in species composition in the south, because of the transitional nature of the northern Baja California area. Greatest similarity of species proportions between inshore-offshore regions generally occurred during the May-July period of maximum OL abundance (Table 6) and reflect dominance by a few summer-spawning species.

Among the 11-regions, only offshore and seaward regions 13 and 14 of northern Baja California did not have significant seasonal OL abundance peaks (Loeb et al. 1983a). These were the only regions that, despite marked seasonal changes in species proportions (i.e., low within-region PSI values; Table 5), had generally high between-region similarities of species proportions throughout the year. They also had similar ranked abundances of their dominant species. These facts imply that more homogeneous environmental conditions existed offshore of northern Baja California than elsewhere in the CalCOFI area during 1975, and probably reflect decreased influence by coastal processes in this locale.

Among the PL species, anchovy and hake most resembled the northern OL species, whereas jack mackerel and sardine were more like the southern OL species, in their distributions and seasonal abundance peaks (Tables 7 and 8). These associations are corroborated by the results of recurrent group analysis on the 1975 ichthyoplankton data (Loeb et al. 1983b). During January-March peak spawning, anchovy and hake in the southern California area had maximum abundances in offshore and seaward regions, while off northern Baja California they were most abundant in inshore regions. These differences were apparently not directly related to coastal upwelling timing or intensity, because the February onset and subsequent spring upwelling intensities were similar in both areas (Bakun and Nelson 1977; Lasker 1978). They may, however, reflect differences in spawning stocks. Apparently, central and southern spawning stocks of the northern anchovy and hake (as well as subpopulations of sardine and jack mackerel) are separated near the northern Baja California coast (Nelson 1977; Vrooman and Paloma 1977; Bakun and Parrish 1980; Hewitt 1981; Parrish et al. 1981).

The northern Baja California area is a transition zone for subarctic/cold-water and eastern tropical Pacific/warm-water fishes, as well as for copepods and euphausiids, and marks a separation of spawning stocks of the major pelagic fish species (Hewitt 1981). It separates areas that have significantly different periods of both zooplankton and OL seasonal abundance peaks (Loeb et al. 1983a). Its inshore regions have concentrations of characteristically offshore zooplankton species plus extreme zooplankton patchiness throughout the year (Arthur 1977; Loeb et al. 1983a). These features may be related to the unique hydrography of the area.

In general, wind-driven surface-layer (Ekman) transport along the coast is directed offshore (positive wind stress curl), creating a coastal divergence or upwelling zone, the extent of which varies seasonally and annually with changes in wind field and intensity. Offshore, surface convergence or downwelling (negative wind stress curl) predominates throughout the year. The boundary between convergence and divergence zones parallels the coast 100-300 km offshore except off northern Baja California (Figure 4; Bakun and Nelson 1977; Parrish et al. 1981). Here a lobe of surface convergence (negative wind stress curl) extends shoreward and impinges on the coast in the Baja California maximum upwelling area between Punta Baja and Punta Eugenia (regions 11 and 12). This feature persists throughout the year and separates the cyclonic eddy of the Southern California Bight and a seasonal coastal eddy south of Punta Eugenia. As indicated by the results presented in this study and in Loeb et al. (1983a), this feature also appears to separate both coastal and offshore biological regimes within the California Current area.

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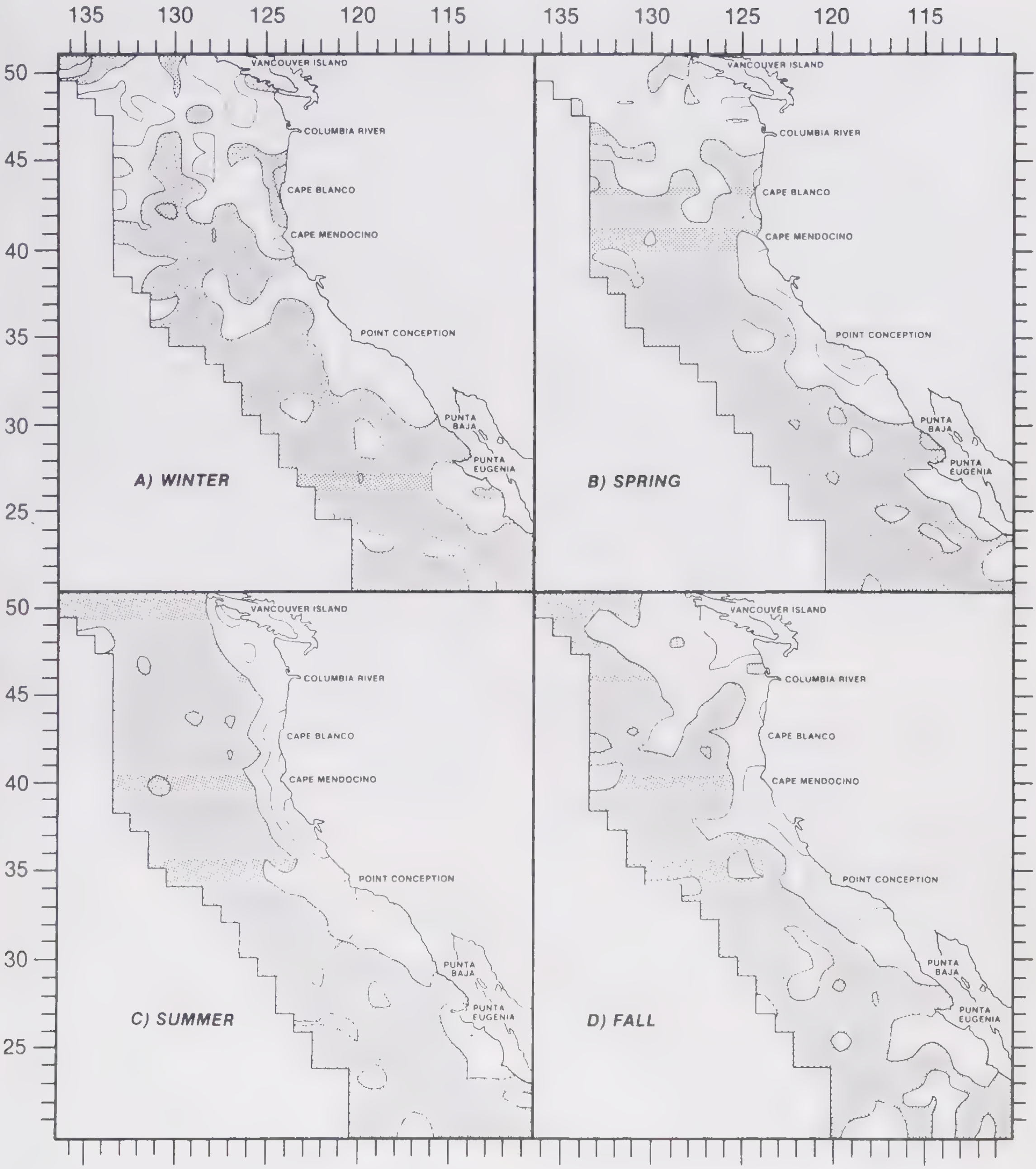

Figure 4. Patterns of wind stress curl, and divergence and convergence zones off California and Baja California, reproduced from Parrish, Nelson, and Bakun (1981). Monthly composite fields of wind stress curl were computed from surface wind stress fields for (*A*) winter (December-February), (*B*) spring (March-May), (*C*) summer (June-August), and (*D*) fall (September-November). The contour interval is 0.25 dyne cm^{2} 100 km. Negative values are shaded and indicate surface Ekman convergence. Unshaded areas indicate surface Ekman divergence

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ICHTHYOPLANKTON AND ZOOPLANKTON ABUNDANCE PATTERNS IN THE CALIFORNIA CURRENT AREA, 1975

VALERIE J. LOEB[1]
San Diego Natural History Museum
P.O. Box 1390
San Diego, California 92112

PAUL E. SMITH AND H. GEOFFREY MOSER
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038

ABSTRACT

The 1975 CalCOFI data were analyzed to provide a description of regional and seasonal zooplankton and ichthyoplankton abundance patterns. Zooplankton and ichthyoplankton abundances were found to be independent of each other on all scales examined. Zooplankton abundance decreased from north to south and inshore to offshore and appeared to be related to distribution of surface nutrient levels. Greatest ichthyoplankton abundance occurred off southern California and northern Baja California and was due to large spawning stocks of migratory species (anchovy, hake, and jack mackerel); the other ichthyoplankton fraction had complex abundance patterns because of its multispecies composition. Seasonal zooplankton abundance fluctuations along the coast (from Punta Eugenia northward) appeared to follow the northward seasonal progression of coastal upwelling. Maximum ichthyoplankton abundance was associated with periods of relatively stable water conditions prior to the onset of intense coastal upwelling. Persistent high-intensity zooplankton patchiness found off northern Baja California is associated with a zone of surface-layer convergence extending to the coast from offshore areas. This convergence zone may mark a separation of southern California and central-southern Baja California coastal biological regimes.

RESUMEN

Se analizaron los datos obtenidos en 1975 durante el programa CalCOFI, con objeto de obtener información sobre la abundancia regional del zooplancton e ictioplancton a lo largo de las estaciones del año. La abundancia de zooplancton no mantenía relación con la abundancia de ictioplancton, a todas las escalas analizadas. La abundancia de zooplancton decrecía de norte a sur y de la zona costera a la oceánica, y aparecía en cierto modo relacionada con la distribución de los nutrientes en las aguas de superficie. La mayor abundancia de ictioplancton se presentaba frente a la parte meridional de California y la zona norte de Baja California, constituyendo el resultado de las grandes concentraciones de poblaciones de especies migratorias (*Engraulis mordax*, *Merluccius productus* y *Trachurus symmetricus*), mientras que la otra porción de ictioplancton presentaba un patrón complejo debido a su composición multiespecífica. Las fluctuaciones en la abundancia del zooplancton a lo largo de las estaciones del año en la zona costera, al norte de Punta Eugenia, siguen al parecer con el avance de la estación, la progresión hacia el norte de las surgencias costeras. La máxima abundancia de ictioplancton aparecía asociada con períodos de estabilidad relativa de las aguas, antes de desencadenarse las intensas surgencias costeras.

Agregaciones persistentes de zooplancton de elevada cuantía se observaron frente a la parte norte de Baja California, asociadas con una zona de convergencia en superficie, extendiéndose desde la costa hasta mar afuera. Esta zona de convergencia pudiera marcar una separación en los regímenes biológicos costeros del sur de California y la parte centro-meridional de Baja California.

INTRODUCTION

Patterns and processes of oceanic life are sketchily known because of the vastness of oceanic regions, the diversity of oceanic biota, and costs of sustained oceanic study. The importance of abundance variations among certain commercially important oceanic fishes led to the field program of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). This program has provided description of hydrographic conditions in coastal waters and the California Current system (Reid et al. 1958) and has collected a vast amount of information on zooplankton and ichthyoplankton abundances in these waters since 1951.

The CalCOFI zooplankton data have been treated by a variety of researchers, and abundance fluctuations of the entire assemblage as well as its major taxa have been related to both short- and long-term physical processes within the California Current system (Reid et al. 1958; Colebrook 1977; Bernal 1980; Chelton 1981, 1982). The ichthyoplankton data have received comparatively little attention. Although abundance fluctuations among a few commercially important species have been examined in detail, the distribution, abundance, and composition of other ichthyoplankton elements have virtually been ignored.

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[1] Current address: Moss Landing Marine Laboratories, P.O. Box 223, Moss Landing, CA 95039.

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Never before have the zooplankton and ichthyoplankton elements been considered together.

Zooplankton and ichthyoplankton are fundamentally different fractions of pelagic communities. Zooplankton individuals spend their entire life cycle as plankton; their distribution and abundance are greatly affected by advective processes within oceanic regions. Larval fishes are the temporary planktonic stages of individuals that are for the most part nektonic and to a large extent zooplanktivorous; ichthyoplankton abundances reflect spawning locales and suitability of conditions for larval survival and recruitment to adult populations. Conditions affecting zooplankton and ichthyoplankton distribution and abundance may be quite different.

Our purpose in this paper is to use the 1975 CalCOFI survey data of zooplankton and ichthyoplankton abundances to identify major seasonal and regional features within the California Current system. Zooplankton and ichthyoplankton abundance patterns are compared to each other and related to physical processes within the current system.

METHODS

The 1975 ichthyoplankton and zooplankton data were derived from standard CalCOFI oblique plankton tows taken with a 1-m diameter net (mesh size, 505 µm) fished from 0 to 210 m. Samples were collected according to the basic CalCOFI station plan (Figure 1), with increased numbers of inshore sampling locations (Lasker 1978). All larval fishes were sorted out, identified, and counted. The larvae of five commercially important pelagic schooling species (anchovy, hake, sardine, jack mackerel, and Pacific mackerel) were sorted and treated separately from the 200+ other larval fish taxa collected. The five species are herein grouped together and referred to as the "PL" ("pelagic" larvae); the remaining taxa are considered together as the "OL" ("other" larvae). Ichthyoplankton abundances used are "total larvae" (all species lumped), the five combined PL species, and the OL fraction. The PL and OL fractions are treated separately because abundances of the PL (especially anchovy and hake) mask abundance relations of the OL. Data on individual PL species are included in tables, figures, and the Appendix, but receive only cursory treatment here; absolute and relative abundances of individual taxa are considered in Loeb et al., 1983a, b. Larval fish abundances are expressed as numbers of larvae per 10 m^{2} sea-surface area; macrozooplankton ($\geqslant$ 5 µm) abundance is wet displacement volume (cc per 1,000 m^{3}) (Kramer et al. 1972).

Absolute regional abundance estimates are mean numbers of larvae per m^{2} sea surface multiplied by sea-surface area of the region. These are summed to provide the total estimated larval fish abundance within the CalCOFI survey area by cruise and for all six 1-month cruises (Appendix).

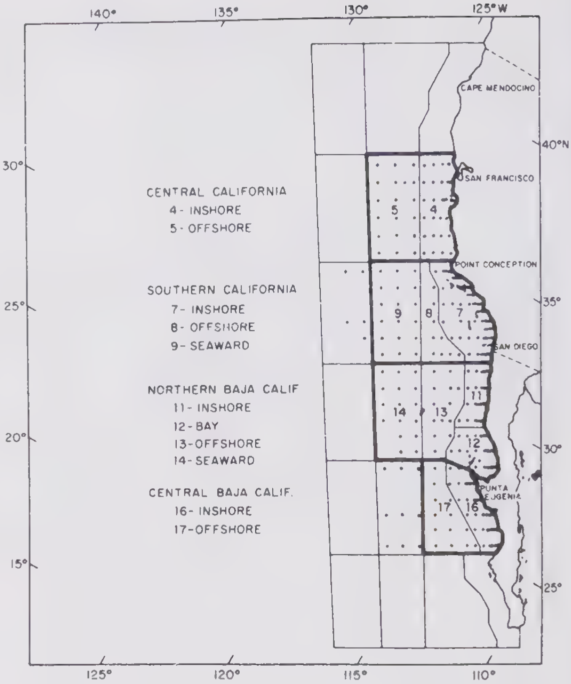

Figure 1. CalCOFI stations, regions, and areas sampled during the 1975 survey.

Data from 1,504 samples were formatted by cruise and standard CalCOFI regions. Thirteen regions were sampled (Figure 1); however, two of these (regions 10 and 18) received relatively less intensive coverage (< 10 samples per region; Table 1) and are not included in the analysis. The 11 regions considered were sampled during at least six 1-month cruises, and most were represented by $\geqslant$ 10 samples per cruise (Table 1). Most regions were sampled in December, January, March, May, July, and October; central California regions 4 and 5 were sampled in November rather than October. November data for southern California regions 7, 8, and 9 were used rather than October data, because larger numbers of samples were available (Table 1). For overviews of abundance and diversity patterns, regional data were combined into four latitudinal areas (central and southern California, northern and central Baja California; Figure 1) and into inshore, offshore, and seaward areas.

Larval fish diversity is expressed in two ways: as the mean number of fish taxa per tow, and as the total number of fish taxa taken in 60 randomly selected

TABLE 1
Regional Sampling Effort, 1975 CalCOFI Survey

		Cruise/month							
Area	Region	7412 Dec.	7501 Jan.	7503 Mar.	7505 May	7507 July	7510 Oct.	7511 Nov.	Total no. samples
Central	4	26	26	23	13	24	—	25	137
California	5	10	4	18	9	12	—	11	64
Southern	7	80	81	81	79	77	7	74	479
California	8	10	8	9	9	9	4	4	53
	9	18	18	16	18	18	—	14	102
	10	2	2	—	—	—	—	—	4
Northern	11	26	26	19	27	26	28	—	152
Baja	12	28	28	18	28	28	29	—	159
California	13	13	13	10	13	13	12	—	74
	14	4	12	4	12	15	15	—	62
Central	16	38	38	18	2	37	37	—	170
Baja	17	13	12	4	1	13	13	—	56
California	18	—	2	1	2	2	2	—	9

samples (10 samples/cruise) from each region. Regions 8 and 17 were represented by 53 and 56 samples, and those diversities may be underestimated.

Sample variability due to patchiness within each region is described by an index of dispersion based on variance to mean ratios ($S^2/\bar{x}$) and compared to an expected chi-square distribution (Pielou 1977). Here chi-square $P \leq 0.05$ implies aggregation, $0.05 < P < 0.95$ implies no significant departure from randomness, and $P \geq 0.95$ implies regularity of distribution. Extremely large index-of-dispersion values reflect high-intensity patchiness (Haury et al. 1978). Index-of-dispersion values for zooplankton abundances are based on biomass, and those of larval fishes are based on numbers of individuals per 10 m^2; consequently, comparisons cannot be made between these values.

Day-night abundance comparisons are based on day (1 hour before sunrise to 1 hour after sunset) and night samples. Differences of these (and other) mean abundances are tested with a 2-tailed Z test (Dixon and Massey 1969).

Comparisons of zooplankton and ichthyoplankton geographical and seasonal abundance patterns are made using Kendall's tau and concordance tests (Tate and Clelland 1957) on ranked regional and cruise abundances. Kendall's tau provides a correlation coefficient that is a measure of the similarity between the order of rankings within two data sets (e.g., between zooplankton and ichthyoplankton ranked regional abundances within a cruise or ranked cruise abundances within a region). The concordance test is a nonparametric analysis of variance performed on several sets of rankings; it is used here to test for similarity of zooplankton, PL, and OL seasonal abundances rankings within areas.

Kolmogorov-Smirnov (K-S) tests (Conover 1971) are based on the maximum differences between cumulative percent curves for two sets of data. They are used here to identify significant differences in the timing of the zooplankton and ichthyoplankton abundance increases.

TAXONOMIC PROBLEMS

The 1,504 samples yielded 104 species, and 100 higher taxa (50 generic, 45 familial, and 5 ordinal). Many abundant larvae (especially the Myctophidae and Bathylagidae) are identified to species, but identification of many coastal larvae, especially *Sebastes* spp (Scorpaenidae) and subtropical forms, is difficult. These identification problems limit analyses, especially the interpretation of diversity indices where inclusion of multispecies groupings certainly underrepresents the actual species richness of a region. This is a major problem only in nearshore and southern regions, but suggests caution in between-region comparisons of diversity.

RESULTS

Abundance and Diversity Estimates

Tables 2 and 3 and the Appendix present 1975 zooplankton and ichthyoplankton abundances by cruise and for all cruises combined for each region. The zooplankton, total larvae, and OL categories all exhibit large sample variances; standard deviations range from 0.3-2.3 times the mean values. Index of dispersion values for zooplankton biomass (Table 4A) and for numbers of total larvae and OL (Table 4B) by region and cruise predominantly indicate extreme aggregations of these categories (X^2 probabilities

≤ 0.05 for 77% of zooplankton, 94% of total larvae, and 85% of OL indices of dispersion). Because of tow-to-tow sample variability caused by patchiness, only large differences in abundance within and between regions can be detected as significant with standard statistical tests.

TABLE 2

Mean and Standard Deviations of Zooplankton Displacement Volume (cc/1000m^3) and Ichthyoplankton Abundance (no./10^2 sea-surface area) by Region and Cruise for 1975

Cruise 7412		Region										
		4	5	7	8	9	11	12	13	14	16	17
Zooplankton	χ	260.7	176.2	85.2	93.4	132.7	85.1	56.6	83.0	53.2	44.5	50.8
	σ	117.0	108.0	49.1	64.1	131.0	70.9	30.6	42.6	11.6	28.9	40.2
Total larvae	χ	132.4	75.7	213.8	83.4	53.2	177.3	93.4	128.1	106.5	679.2	70.4
	σ	247.0	68.9	201.0	100.0	33.7	236.0	119.0	58.4	127.0	884.0	87.1
Anchovy	χ	2.2	8.5	123.2	9.4	—	88.4	62.0	4.5	—	597.6	—
	σ	4.6	18.4	154.0	18.3	—	180.0	112.0	9.0	—	878.0	—
Hake	χ	0.9	—	1.8	—	—	—	—	—	—	0.6	—
	σ	3.1	—	0.8	—	—	—	—	—	—	1.8	—
Sardine	χ	—	—	—	—	—	—	—	—	—	7.5	—
	σ	—	—	—	—	—	—	—	—	—	20.8	—
Other larvae	χ	129.3	67.2	88.8	74.0	53.2	88.9	31.4	123.6	106.5	73.5	70.4
	σ	247.0	53.6	135.0	84.7	33.7	80.6	34.8	61.7	127.0	64.7	87.1
No. tows		26	10	80	10	18	26	28	13	4	38	13
Cruise 7501		Region										
		4	5	7	8	9	11	12	13	14	16	17
Zooplankton	χ	206.6	117.5	104.8	89.1	84.2	159.5	130.3	62.2	68.7	51.4	42.8
	σ	152.0	40.0	55.2	35.5	58.4	174.0	83.3	20.7	31.6	41.0	23.4
Total larvae	χ	425.0	127.5	1943.3	4628.4	1886.9	2183.2	2539.1	2133.1	193.8	625.3	201.8
	σ	344.0	122.0	2155.0	2730.0	4248.0	4341.0	4293.0	3096.0	92.5	1443.0	296.0
Anchovy	χ	11.8	—	1463.5	4027.0	189.9	1997.1	2374.5	2059.5	24.2	554.6	109.1
	σ	24.5	—	2123.0	3123.0	584.0	4320.0	4166.0	3097.0	35.9	1438.0	272.0
Hake	χ	28.9	—	89.0	449.2	1593.0	25.9	1.3	5.5	—	5.6	1.0
	σ	55.6	—	370.0	833.0	4120.0	50.7	5.1	14.0	—	10.5	3.5
Jack mackerel	χ	—	—	0.2	—	—	—	—	—	—	—	—
	σ	—	—	1.4	—	—	—	—	—	—	—	—
Sardine	χ	—	—	—	—	—	—	7.5	—	—	8.7	—
	σ	—	—	—	—	—	—	17.2	—	—	39.3	—
Other larvae	χ	384.3	127.5	390.7	152.1	104.0	160.2	155.8	68.2	169.6	56.6	91.7
	σ	328.0	122.0	433.0	119.0	60.8	134.0	152.0	34.8	96.2	69.8	73.5
No. tows		26	4	81	8	18	26	28	13	12	38	12
Cruise 7503		Region										
		4	5	7	8	9	11	12	13	14	16	17
Zooplankton	χ	187.1	143.6	284.1	145.4	115.4	346.3	488.7	94.9	63.8	252.9	97.0
	σ	80.5	121.0	208.0	61.0	61.6	454.0	389.0	45.8	39.1	198.0	24.0
Total larvae	χ	311.1	151.0	2494.4	2721.4	659.9	2857.9	2112.8	941.9	876.2	1656.2	1307.3
	σ	203.0	102.0	2405.0	2665.0	1113.0	1931.0	3845.0	1036.0	1056.0	1911.0	1263.0
Anchovy	χ	1.9	0.4	2047.4	1973.4	15.3	2054.0	1883.6	313.2	2.5	1569.1	1068.5
	σ	5.1	1.9	2344.0	2178.0	40.1	1768.0	3755.0	688.0	3.3	1882.0	1345.0
Hake	χ	2.0	1.1	82.8	548.3	525.0	617.0	36.3	529.1	297.8	5.7	1.8
	σ	4.0	3.1	269.0	978.0	1053.0	957.0	58.5	921.0	541.0	8.4	3.5
Jack mackerel	χ	—	0.2	—	—	8.3	4.6	1.3	22.0	333.5	2.4	13.5
	σ	—	0.7	—	—	21.7	13.2	3.9	19.0	414.0	6.0	20.3
Sardine	χ	—	—	0.7	—	—	—	—	—	—	—	—
	σ	—	—	0.7	—	—	—	—	—	—	—	—
Other larvae	χ	307.1	149.3	364.1	199.7	111.3	182.4	191.6	77.6	242.5	79.1	223.5
	σ	203.0	101.0	318.0	182.0	97.8	106.0	335.0	43.3	276.0	69.5	226.0
No. tows		23	18	81	9	16	19	18	10	4	18	4

Continued on next page

TABLE 2 (Cont.)

Mean and Standard Deviations of Zooplankton Displacement Volume (cc/1000m^3) and Ichthyoplankton Abundance (no./10^2 sea-surface area) by Region and Cruise for 1975

Cruise 7505		Region										
		4	5	7	8	9	11	12	13	14	16	17
Zooplankton	χ	338.7	258.8	322.9	512.0	203.1	486.9	196.4	172.2	88.9	177.0	—
	σ	397.0	174.0	463.0	568.0	160.0	618.0	124.0	91.3	28.0	42.4	—
Total larvae	χ	103.2	119.1	293.8	76.4	97.3	1396.1	1510.8	248.0	221.2	1319.5	400.0
	σ	83.4	75.7	410.0	57.0	69.3	2527.0	3549.0	195.0	126.0	251.0	—
Anchovy	χ	2.9	—	243.0	2.7	—	1324.3	1210.1	60.1	0.5	1186.0	—
	σ	10.5	—	404.0	5.7	—	2504.0	3067.0	161.0	1.7	124.0	—
Hake	χ	2.7	11.2	0.04	—	1.6	0.4	—	1.0	—	—	—
	σ	4.6	17.6	0.34	—	3.1	2.1	—	3.6	—	—	—
Jack mackerel	χ	—	—	—	—	—	5.3	0.3	76.0	10.8	—	—
	σ	—	—	—	—	—	9.9	1.7	112.0	9.6	—	—
Sardine	χ	—	—	—	—	—	—	6.9	—	—	—	—
	σ	—	—	—	—	—	—	36.5	—	—	—	—
Other larvae	χ	97.6	107.9	50.8	73.8	95.7	66.2	293.5	110.9	210.0	133.5	400.0
	σ	78.3	61.6	49.0	59.0	68.0	60.7	530.0	60.7	124.0	127.0	—
No. tows		13	9	79	9	18	27	28	13	12	2	1

Cruise 7507		Region										
		4	5	7	8	9	11	12	13	14	16	17
Zooplankton	χ	276.9	292.8	165.3	179.4	197.6	179.3	169.1	78.8	50.5	118.5	64.3
	σ	194.0	259.0	199.0	124.0	123.0	292.0	166.0	35.7	19.5	121.0	67.3
Total larvae	χ	62.4	56.1	198.9	119.2	79.9	331.9	641.0	228.9	343.5	284.5	343.7
	σ	44.0	43.0	281.0	124.0	59.1	621.0	996.0	298.0	233.0	341.0	293.0
Anchovy	χ	1.5	—	163.6	3.7	0.2	263.2	160.2	17.4	0.1	68.0	34.0
	σ	5.0	—	277.0	9.9	0.7	580.0	216.0	25.8	0.5	175.0	121.0
Hake	χ	—	—	—	—	—	—	1.7	—	0.2	0.1	—
	σ	—	—	—	—	—	—	4.0	—	0.8	0.6	—
Jack mackerel	χ	—	1.2	0.7	49.3	18.3	2.7	—	12.6	17.5	1.1	0.2
	σ	—	4.3	4.1	127.0	19.9	6.4	—	11.9	13.5	3.9	0.6
Sardine	χ	—	—	—	—	—	—	0.2	—	—	20.3	—
	σ	—	—	—	—	—	—	0.9	—	—	71.5	—
Other larvae	χ	61.0	54.8	34.6	66.2	61.4	66.0	478.9	198.9	325.7	194.9	309.4
	σ	42.7	41.7	34.1	28.6	50.5	64.2	864.0	300.0	238.0	261.0	248.0
No. tows		24	12	77	9	18	26	28	13	15	37	13

Cruise 7510		Region										
		4	5	7	8	9	11	12	13	14	16	17
Zooplankton	χ	—	—	139.7	40.2	—	126.0	118.1	45.6	43.8	112.4	105.9
	σ	—	—	86.4	34.5	—	211.0	132.0	23.2	27.6	93.5	108.0
Total larvae	χ	—	—	684.9	53.5	—	101.5	357.1	79.9	182.4	334.8	182.7
	σ	—	—	448.0	61.0	—	88.9	463.0	33.4	140.0	376.0	202.0
Anchovy	χ	—	—	293.1	30.8	—	23.0	136.3	—	0.8	104.9	27.7
	σ	—	—	219.0	61.5	—	44.7	297.0	—	2.6	229.0	96.6
Hake	χ	—	—	—	—	—	—	0.2	0.2	—	—	—
	σ	—	—	—	—	—	—	0.9	0.9	—	—	—
Jack mackerel	χ	—	—	—	1.2	—	0.5	0.1	—	—	—	—
	σ	—	—	—	2.5	—	1.5	0.4	—	—	—	—
Sardine	χ	—	—	—	—	—	0.7	17.5	—	—	5.0	—
	σ	—	—	—	—	—	2.8	27.1	—	—	13.3	—
Pacific mackerel	χ	—	—	—	—	—	—	1.2	—	—	1.5	—
	σ	—	—	—	—	—	—	4.5	—	—	5.2	—
Other larvae	χ	—	—	391.7	21.5	—	77.4	201.9	79.7	181.6	223.3	154.9
	σ	—	—	311.0	13.2	—	66.3	304.0	33.6	138.0	223.0	189.0
No. tows		—	—	7	4	—	28	29	12	15	37	13

Continued on next page

TABLE 2 (Cont.)

Mean and Standard Deviations of Zooplankton Displacement Volume (cc/1000m^3) and Ichthyoplankton Abundance (no./10^2 sea-surface area) by Region and Cruise for 1975

Cruise 7511		Region 4	5	7	8	9	11	12	13	14	16	17
Zooplankton	χ	254.2	105.4	107.6	74.2	91.6						
	σ	252.0	59.0	96.5	44.1	88.3						
Total larvae	χ	78.8	32.1	337.5	63.0	68.0						
	σ	55.5	15.8	339.0	35.1	64.8						
Anchovy	χ	0.1	—	292.7	—	1.5						
	σ	0.4	—	335.0	—	2.8						
Hake	χ	—	—	1.6	—	—						
	σ	—	—	4.8	—	—						
Jack mackerel	χ	—	—	0.03	—	—						
	σ	—	—	0.23	—	—						
Sardine	χ	—	—	0.04	—	—						
	σ	—	—	0.35	—	—						
Other larvae	χ	78.8	32.1	43.1	63.0	66.5						
	σ	55.5	15.8	34.6	35.1	64.7						
No. tows		25	11	74	4	14						

Ichthyoplankton abundances given for total larvae, 5 species constituting the PL, and other larvae (OL).

TABLE 3

Mean and Standard Deviations of Zooplankton Displacement Volume (cc/1000m^3) and Ichthyoplankton Abundance (no./10m^2 sea-surface area) for All Samples Taken Within Each of 11 CalCOFI Regions (6 Cruises Total) during 1975

		Region 4	5	7	8	9	11	12	13	14	16	17
Zooplankton	χ	247.2	184.7	179.1	183.6	139.7	225.5	174.1	89.8	60.9	100.6	70.0
	σ	203.0	164.0	245.0	282.0	119.0	372.0	207.0	63.2	30.6	116.0	68.9
Total larvae	χ	193.1	95.0	932.3	1241.2	486.5	1084.5	1146.8	621.3	271.1	617.3	282.3
	σ	246.0	85.7	1653.0	2290.0	1922.0	2404.0	2816.0	1515.0	329.0	1102.0	457.0
Anchovy	χ	3.5	1.4	736.6	966.4	363.8	898.0	908.5	418.5	5.2	475.3	117.6
	σ	12.2	7.6	1528.0	2089.0	1840.0	2310.0	2638.0	1494.0	18.0	1096.0	437.0
Hake	χ	6.3	1.9	30.0	164.0	4.5	81.6	4.7	72.7	19.3	2.0	0.3
	σ	26.4	7.5	193.0	550.0	13.7	388.0	22.5	371.0	141.0	6.2	1.8
Jack mackerel	χ	—	0.3	0.1	8.6	—	2.0	0.2	18.5	27.8	0.5	1.0
	σ	—	1.9	1.8	53.6	—	7.0	1.5	53.9	123.0	2.7	5.9
Sardine	χ	—	—	0.02	—	—	0.13	5.8	—	—	9.1	—
	σ	—	—	0.31	—	—	1.19	21.2	—	—	40.0	—
Pacific mackerel	χ	—	—	—	—	—	—	0.21	—	—	0.34	—
	σ	—	—	—	—	—	—	1.95	—	—	2.45	—
PL	χ	9.8	3.6	766.8	1139.0	404.4	981.8	919.3	509.7	52.3	487.2	119.0
	σ	32.3	10.7	1563.0	2265.5	1904.0	2372.0	2640.0	1522.0	259.0	1098.0	439.0
OL	χ	183.3	91.4	165.5	102.1	82.1	102.7	227.5	111.5	218.7	130.0	163.3
	σ	235.0	82.1	277.0	111.0	67.0	97.3	478.0	137.0	176.0	181.0	188.0
No. tows		137	64	472	53	102	152	159	74	62	170	56
							Ranked regional abundance					
Total larvae		10	11	4	1	7	3	2	5	9	6	8
PL		10	11	4	1	7	2	3	5	9	6	8
OL		3	10	4	9	11	8	1	7	2	6	5

Ichthyoplankton abundances given for total larvae, 5 species constituting the PL, and other larvae (OL). Regional ranks provided for total, PL, and OL abundances.

TABLE 4
Index of Dispersion Values for (A) Zooplankton Biomass and (B) Total Larval Fish (TL) and OL Abundances Within 11 CalCOFI Regions by Cruise

		Region										
		Central California		Southern California				Northern Baja California			Central Baja California	
		4	5	7	8	9	11	12	13	14	16	17
A. Zooplankton Cruise												
7412		52.5	66.2	(28.3)	44.0	129.3	59.1	16.5	21.6	(2.5)	(18.8)	31.8
7501		111.8	13.6	(29.1)	14.1	40.5	189.8	53.2	(6.9)	(14.5)	(32.7)	(12.8)
7503		34.6	102.0	152.3	25.6	32.9	595.2	309.6	22.1	24.0	155.0	(5.9)
7505		465.3	117.0	663.9	630.1	126.0	784.4	78.3	48.4	(8.8)	10.2	—
7507		135.9	229.1	239.6	85.7	76.6	475.5	169.9	(16.2)	(7.5)	123.6	70.4
7510 (11)		249.8	33.0	(86.5)	26.2	85.1	353.3	147.5	(11.8)	(17.4)	77.8	110.1
B. Total larvae and OL Cruise												
7412	TL	460.8	62.9	189.0	119.9	(21.3)	314.1	151.6	26.6	151.4	1150.5	107.8
	OL	471.8	42.8	205.2	96.9	(21.3)	73.1	(38.6)	30.8	151.4	57.0	107.8
7501	TL	278.4	116.7	2389.8	1610.2	9563.6	8631.5	7258.4	4493.6	44.1	3330.0	434.2
	OL	280.0	116.7	479.9	93.1	35.5	112.1	148.3	(17.8)	54.6	86.1	58.9
7503	TL	132.5	68.9	2318.8	2609.8	1877.2	1304.7	6638.1	1139.5	1272.7	2205.0	1220.2
	OL	134.2	68.3	277.7	165.9	85.9	61.6	585.7	24.2	314.1	61.0	228.5
7505	TL	67.4	48.1	572.2	42.5	49.4	4574.0	8336.9	153.3	71.8	47.7	—
	OL	62.8	35.2	(47.3)	47.2	48.3	55.7	957.1	33.2	73.2	120.8	—
7507	TL	(31.0)	32.9	397.0	129.0	43.7	1161.9	1547.6	389.9	158.0	408.7	249.8
	OL	(29.9)	31.7	(33.6)	(12.4)	41.5	62.4	1558.8	452.5	173.9	349.5	198.8
7510(11)	TL	39.1	(7.8)	340.5	19.6	61.8	77.9	600.3	(14.0)	107.5	422.3	223.3
	OL	39.1	(7.8)	(27.8)	19.6	62.9	56.8	457.7	(14.2)	104.9	222.7	230.6

Values within parentheses indicate nonsignificant departures ($P > 0.05$) from random distribution.

Larval fish diversity is presented in Table 5 as (A) mean numbers of taxa per tow and (B) total numbers of taxa in 60 tows within each region. Mean numbers of larval fish taxa per tow varied much less than larval abundance values (standard deviations 0.3-0.7 times mean values) and reflect relatively constant regional diversities within each cruise. Between-cruise mean diversity values generally varied ≤ than a factor of 2 within each region. The two overall diversity measurements indicate similar regional trends and have a rank difference correlation coefficient (Tate and Clelland 1957), calculated across all regions, of 0.714 ($P < 0.05$).

Day-Night Differences in Abundance and Diversity

Day-night catch differences may bias abundance and diversity estimates. Bridger (1956) and Ahlstrom (1959) reported night:day ratios of ~ 3:1 for total (mixed taxa) larval fish abundances, and attributed these differences to daytime net avoidance. Consistent catch differences of this magnitude could introduce large errors in abundance estimates based on combined day and night data. Z tests were performed on mean day and mean night abundance values of each larval fish category by region and cruise and for the combined total of regions and cruises (Table 6). Only 33 of 183 day-night abundance comparisons were significantly different; in 6 cases day catches were larger, and in 27 cases night catches were larger. Twenty-three percent of the comparisons in the total larvae and OL categories yielded significant differences. Nine of the 13 significant night:day catch differences of total larvae were associated with significant catch differences of OL rather than PL categories. Significant day-night catch differences in the combined regional data occurred only within the total larvae and OL categories (Table 6). The ratio of night:day catches of zooplankton and ichthyoplankton varied widely within each region (Table 6). For most categories night catches were generally (but not significantly) larger than day catches. Night:day ratios were: total larvae, anchovy, and OL all 1.3:1; hake, 2.2:1; jack mackerel, 2.4:1. Zooplankton had a 1:1 night:day ratio. Night tows also generally yielded more larval fish taxa per tow (overall night:day ratio = 1.3:1); 11 of 61 comparisons were significant, and all 11 showed greater night than day catches.

Overview of Abundance and Diversity in the CalCOFI Area

Zooplankton abundance decreased from north to south and from inshore to offshore (Table 7; Figure 2). Mean zooplankton abundance off central California was significantly higher, and off central Baja California significantly lower, than in the other two areas ($P < 0.01$, Z test). Maximum mean and absolute

TABLE 5

Larval Fish Diversity Expressed as (A) Mean and Standard Deviations of Numbers of Larval Taxa per Tow by Region and Cruise and as (B) the Total Numbers of Larval Taxa Taken in 60 Samples Within Each Region

Cruise		Region										
A.		4	5	7	8	9	11	12	13	14	16	17
7412	X	4.3	3.6	4.6	6.6	6.0	5.3	3.6	6.8	10.0	5.6	4.5
	σ	2.4	1.6	2.4	3.6	3.6	2.9	1.7	3.3	5.7	2.6	3.1
No. tows		27	10	80	10	18	26	28	13	4	38	13
7501	X	7.3	6.0	6.7	7.9	10.9	7.6	6.3	7.3	14.9	5.6	6.9
	σ	2.8	4.1	2.2	4.0	4.0	2.3	2.1	3.4	3.0	2.9	1.9
No. tows		26	4	81	8	18	26	28	13	12	38	12
7503	X	6.7	8.3	7.8	8.3	11.8	8.6	5.1	7.0	15.2	4.9	7.5
	σ	2.9	4.7	2.8	3.8	5.0	3.0	3.6	1.5	9.0	1.8	3.7
No. tows		23	18	81	9	16	19	17	10	4	18	4
7505	X	5.1	7.0	4.1	4.9	10.3	4.5	5.4	7.0	12.8	5.5	9.0
	σ	2.3	4.8	2.5	3.5	5.3	2.2	2.6	2.8	3.4	3.5	—
No. tows		13	9	79	9	18	27	28	13	12	2	1
7507	X	2.5	4.5	3.9	7.0	9.8	5.1	6.3	6.7	14.7	6.0	9.3
	σ	1.8	2.0	2.4	4.6	5.7	2.2	2.2	3.8	4.5	3.8	4.8
No. tows		24	12	77	9	18	26	28	13	15	37	13
7510	X	—	—	6.9	5.2	7.0	6.9	7.6	8.7	12.2	10.6	6.8
	σ	—	—	3.1	1.5	3.0	3.7	4.2	4.9	4.6	5.3	4.8
No. tows		—	—	7	4	3	28	29	12	15	37	13
7511	X	3.1	2.9	5.1	6.8	8.9	—	—	—	—	—	—
	σ	1.4	1.9	2.8	5.2	5.5	—	—	—	—	—	—
No. tows		25	11	74	4	14	—	—	—	—	—	—
Total	X	4.8	5.6	5.4	6.7	9.5	6.2	5.8	7.2	13.5	6.6	7.0
	σ	2.9	4.0	2.9	3.9	5.1	3.1	3.0	3.4	4.6	4.1	4.0
No. tows		137	64	472	53	105	152	159	74	62	170	56
Region rank (total means)		11	9	10	5	2	7	8	3	1	6	4

	Region										
B.	4	5	7	8	9	11	12	13	14	16	17
No. taxa in 60 tows (* denotes < 60 tows)	49	62	51	62*	80	74	77	67	99	77	73*
Region rank	11	8.5	10	8.5	2	5	3.5	7	1	3.5	6

ichthyoplankton abundances occurred in the areas off southern California and northern Baja California; about 39% of the total estimated larval abundance was from each of these areas, whereas the central Baja California area yielded about 17% of the total, and only 5% of the total larvae occurred north of Point Conception. Mean larval fish abundances decreased from inshore to offshore and seaward areas (Table 7; Figure 3). Mean numbers of larval fish taxa/tow increased from north to south, reaching maximum levels off northern Baja California (Table 7; Figure 4). Unlike abundance, diversity increased with distance from shore, perhaps partly because of better identification ability for larvae of offshore fish species.

Regions differed in total larval fish abundance and in the relative abundances of the PL and OL fractions. Total larval abundances were highest in regions 7, 11, and 12 of southern California and northern Baja California and region 8 of southern California because of large numbers of PL (Figures 3 and 5). Here the PL (primarily anchovy) made up ≥ 80% of the regional totals (Table 3). Anchovy-dominated PL also constituted > 80% of the relatively moderate larval fish abundances of central Baja California region 16 and regions 9 and 13 of southern California and northern Baja California (Figures 3 and 5; Table 3). Total larval abundances were relatively low (Figure 3), and the proportions of PL and OL more similar, in regions 14 and 17 of northern and central Baja California. The PL of region 17 was primarily anchovy, whereas that of region 14 was mostly jack mackerel and hake (Table 3). Central California regions 4 and 5 had the lowest

TABLE 6

Results of Comparisons of Day and Night Catches of Zooplankton, Total Larvae, 5 Species of PL, and the Other Larvae (OL), and the Ratio of Night:Day Abundances of These Categories for (A) Individual Region and Cruise Data (239 Comparisons) and (B) Combined Region and Cruise Data (850 Day Samples, 636 Night Samples)

				Regional data				
	Zooplankton volume	Total larvae	Anchovy	Hake	Jack mackerel	Sardine	Pacific mackerel	Other larvae
No. signif. differences	9	13	2	2	1	2	0	13
No. comparisons	56	56	37	21	9	3	1	56
No. signif. larger day values	1	2	1	2	—	1	—	—
No. signif. larger night values	8	11	1	—	1	1	—	13
				Ratio of night:day abundance values				
Range	0.7-1.5	0.7-2.5	0.6-20	0.3-4.4	0.8-5.5	0.4-7.7	0.5	0.7-2.0
Mean	1.1:1	1.4:1	1.1:1	1.7:1	2.6:1	4.0:1	0.5:1	1.4:1
B.				Combined region and cruise data				
Probability level for signif. differences	$P=0.63$	$P=0.03$*	$P=0.16$	$P=0.19$	$P=0.15$	$P=0.55$	$P=0.39$	$P=0.003$*
Ratio night:day	1.0:1	1.3:1	1.3:1	2.2:1	2.4:1	0.8:1	0.4:1	1.3:1

Significance of abundance differences are based on the Z test ($P < 0.05$; 2 tailed); asterisk denotes significant comparisons.

TABLE 7

Areal Summary of Means and Standard Deviations of Zooplankton and Ichthyoplankton Abundances and of Ichthyoplankton Diversity Within the 1975 CalCOFI Survey Area

CalCOFI area	Zooplankton abundance (cc/1000m^3)	Ichthyoplankton abundance (no./10m^2)	Percentage of total CalCOFI area ichthyoplankton	Larval fish diversity (mean no. taxa/tow)
I: Central California (regions 4, 5; 46,599 nmi^2) 201 samples	227 ± 193	162 ± 214	4.98%	5.2
II: Southern California (regions 7, 8, 9; 60,906 nmi^2) 626 samples	173 ± 233	885 ± 1767	39.40%	7.2
III: Northern Baja California (regions 11, 12, 13, 14; 69,394 nmi^2) 447 samples	162 ± 258	917 ± 2293	38.16%	8.2
IV: Central Baja California (regions 16, 17; 36,653 nmi^2) 226 samples	93 ± 107	534 ± 994	17.46%	6.8
Inshore (regions 4, 7, 11, 12, 16; 72,024 nmi^2) 1,090 samples	181 ± 246	843 ± 1848	47.36%	5.8
Offshore (regions, 5, 8, 13, 17; 83,964 nmi^2) 246 samples	130 ± 168	538 ± 1415	33.62%	6.4
Seaward (regions 9, 14; 57,564 nmi^2) 164 samples	110 ± 103	405 ± 1530	19.02%	11.5

Areal estimates based on combined (6 cruises) regional sample data (regions are noted for each area considered). Zooplankton abundance as mean displacement volume (cc/1000m^3); ichthyoplankton abundance as mean numbers of larvae/10 m^2 sea-surface area and as the percentage of the total estimated numbers of larvae represented by each area; and larval fish diversity as mean numbers of larval taxa/tow. Regional areas given as numbers of square nautical miles.

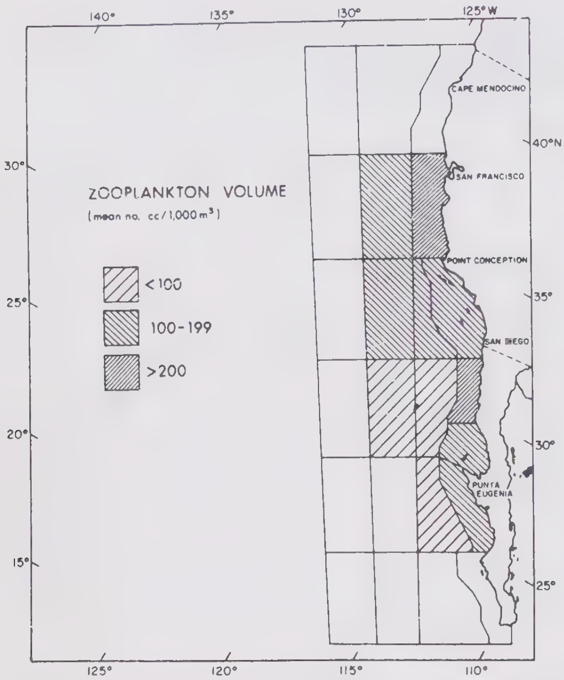

Figure 2. Mean zooplankton volume in 11 CalCOFI regions sampled during 1975.

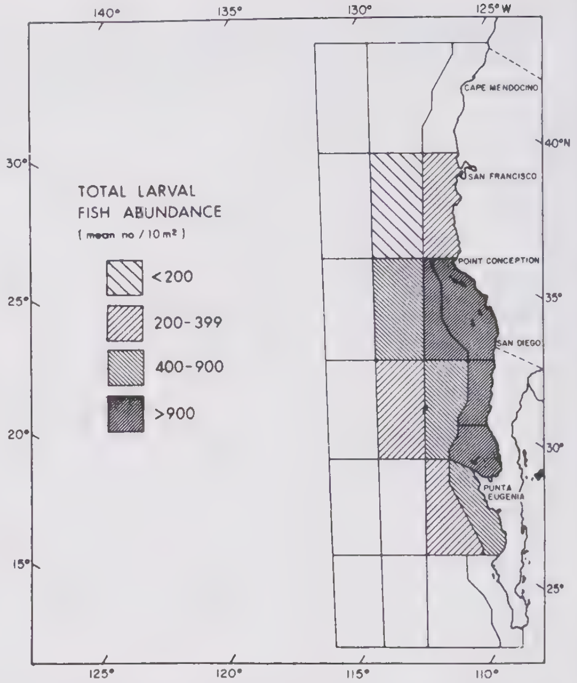

Figure 3. Mean larval fish abundance (total) in 11 CalCOFI regions sampled during 1975.

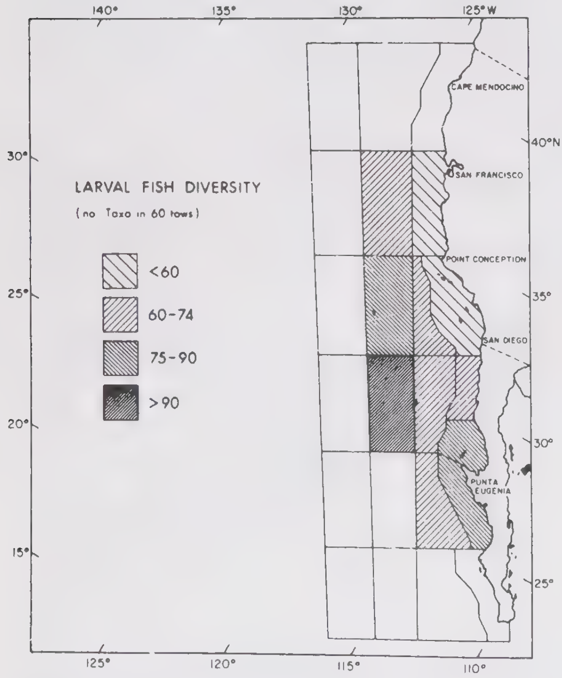

Figure 4. Larval fish diversity in 11 CalCOFI regions sampled during 1975. Diversity expressed as numbers of larval taxa taken in 60 samples within each region.

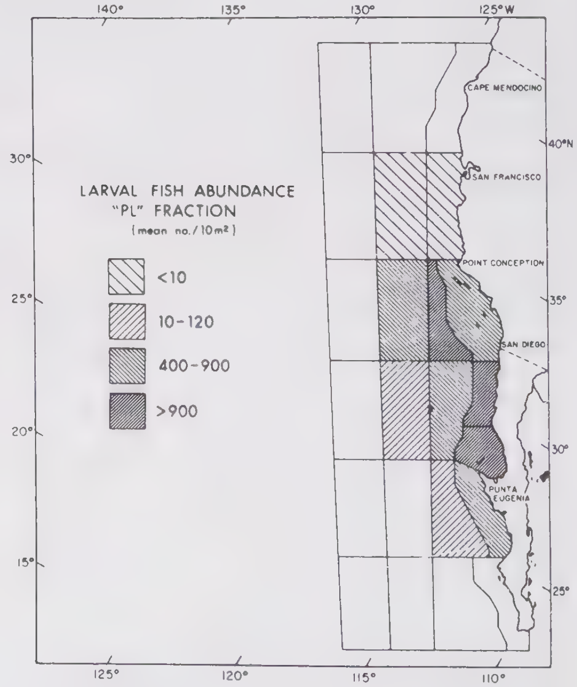

Figure 5. Mean larval fish abundance (PL fraction) in 11 CalCOFI regions sampled during 1975.

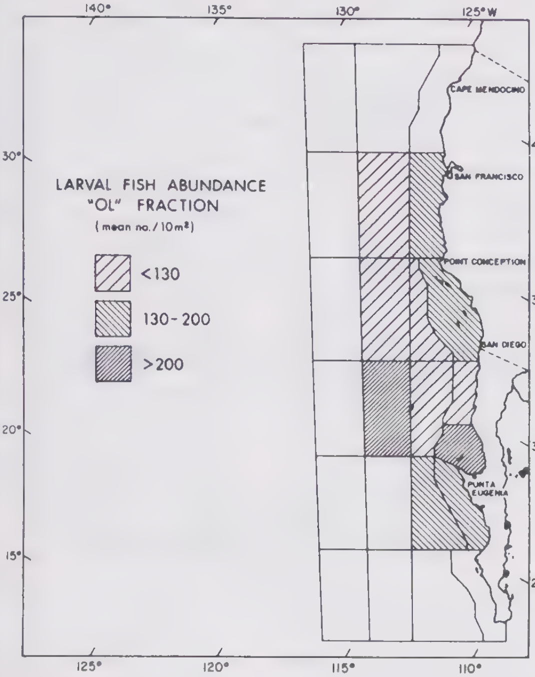

Figure 6. Mean larval fish abundance (OL fraction) in 11 CalCOFI regions sampled during 1975.

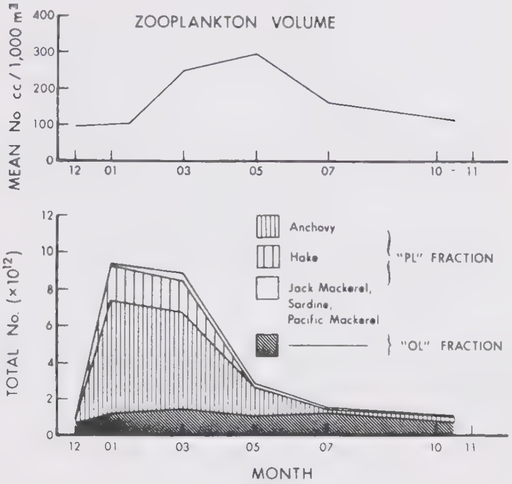

Figure 7. Seasonal variation in zooplankton volume and abundance of major ichthyoplankton components in CalCOFI area during 1975

concentrations of larvae; absolute abundances here were an order of magnitude lower than in the south, and the PL made up only a small proportion (< 5%) of the total larvae.

Largest mean OL abundances occurred off northern Baja California in Viscaino Bay region 12 (because of flatfishes) and in seaward region 14 (because of mesopelagic fishes) (Figure 6). Absolute OL abundances were highest in northern and central Baja California regions 14 and 17 (19% and 15% of the total CalCOFI OL, respectively). Inshore southern California region 7, although dominated by PL, also contributed 12% of the total OL (Appendix). Although regions 4 and 5 were dominated by OL species, they contributed only 10% and 8% to the total OL.

Maximum larval fish diversity (both numbers of taxa per tow and numbers of taxa per 60 tows within a region) occurred off northern Baja California in seaward region 14 (Table 5, Figure 4) in association with maximum OL abundance. Southern California seaward region 9 ranked second in diversity, but had only moderate OL abundances. The mean numbers of larval fish taxa per tow in these two regions were significantly higher than in all other regions ($P << 0.01$). Minimal diversity values occurred off central and southern California in regions 4, 5, and 7.

Seasonal Changes in Abundance: Areal Overview

Ichthyoplankton and zooplankton abundances underwent large seasonal fluctuations (Figure 7). Maximum larval fish abundances were found during January and March cruises, which captured > 60% of the total (summed six cruises) estimated numbers of larvae. This was due to peak abundances of two PL species—anchovy and hake (Figure 7). This larval abundance peak preceded maximum zooplankton abundance (March and May). The OL abundances from January through July were about twice the October-November and December values. Although the OL made up only a small proportion (≤ 16%) of the total absolute larval abundance during the January-March PL abundance peak, the proportion increased from May to November (May, 39%; July 75%; October-November, 68%) because of decreased PL abundances.

There were north-south differences in seasonal abundance peaks of zooplankton and larval fish (Figure 8). Northern zooplankton peaks occurred later, and northern ichthyoplankton peaks earlier, than their southern counterparts. Off central California, maximum zooplankton abundances were in May and July; off southern California, during May; off northern and central Baja California, during March. Central California peak larval abundances (almost entirely due to OL) occurred during January and March. Southern California peak OL and PL abundances were also in January and March, but the PL dominated. The northern Baja California area had a longer (January-May) period of elevated PL abundance, and a much later (July) OL abundance peak, than did the southern Cali-

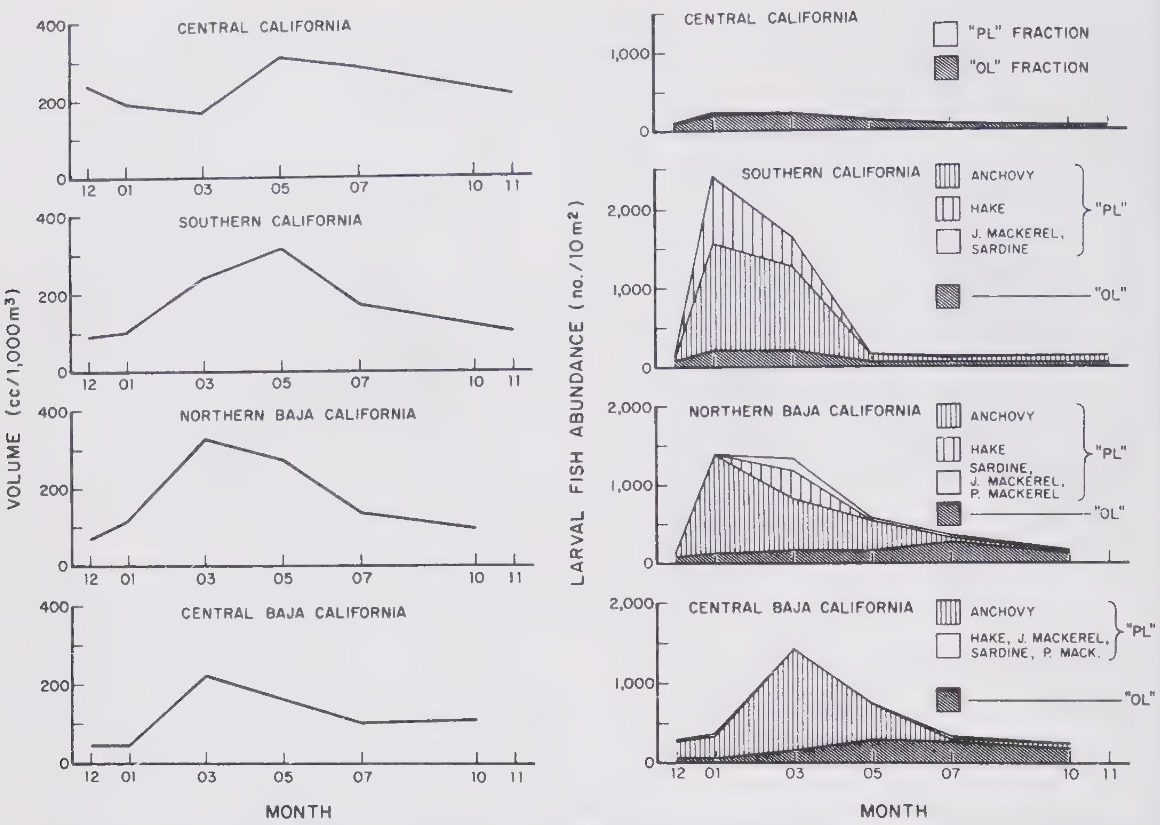

Figure 8. Seasonal variation in zooplankton volume and abundance of major ichthyoplankton components in four latitudinal portions of the CalCOFI area during 1975. Zooplankton abundance (mean displacement volume) based on combined regional sample data for each cruise; ichthyoplankton abundance as estimated total numbers of larvae of each component within each area (summed regional abundance estimates corrected for region surface area) by cruise.

fornia area. Off central Baja California, peak abundances of PL occurred during March, of OL during May and July. Seasonal ichthyoplankton and zooplankton abundance peaks within each area occurred during different months in all but the central Baja California area (Figure 8). Off southern California and northern Baja California, PL abundance peaks occurred before zooplankton abundance peaks. Peak OL abundances off central and southern California preceded, and off northern Baja California followed, peak zooplankton abundances. Off central Baja California, PL and zooplankton abundance peaks coincided; these preceded the OL abundance peak.

Seasonal Changes in Abundance and Diversity

Central California: regions 4 and 5. Central California regions 4 and 5 had similar abundance patterns (Figure 9), although zooplankton and ichthyoplankton abundance peaks in offshore region 5 occurred later than those of inshore region 4. The OL dominated the ichthyoplankton throughout the year in both regions. Significant peak larval abundances ($P < 0.01$; Z test) occurred in region 4 during January and March. Elevated, but significantly lower, abundance values occurred in region 5 at this time and extended through May. In both regions highest larval fish diversity values were associated with the months of maximum larval abundance. Zooplankton abundance within region 4 remained at fairly high levels throughout the year. Within region 5, May and July zooplankton abundances were significantly higher than during other months.

Southern California: regions 7, 8, and 9. The three southern California regions had peak PL and OL abundances during January and March (Figure 10). Inshore region 7 differed from the others by having a second (similar in value) OL peak in November and by having PL (primarily anchovy) dominate the ichthyoplankton throughout the year. Here the PL made up $> 58\%$, and during most months $>80\%$, of the total larvae. In contrast, the PL of offshore and

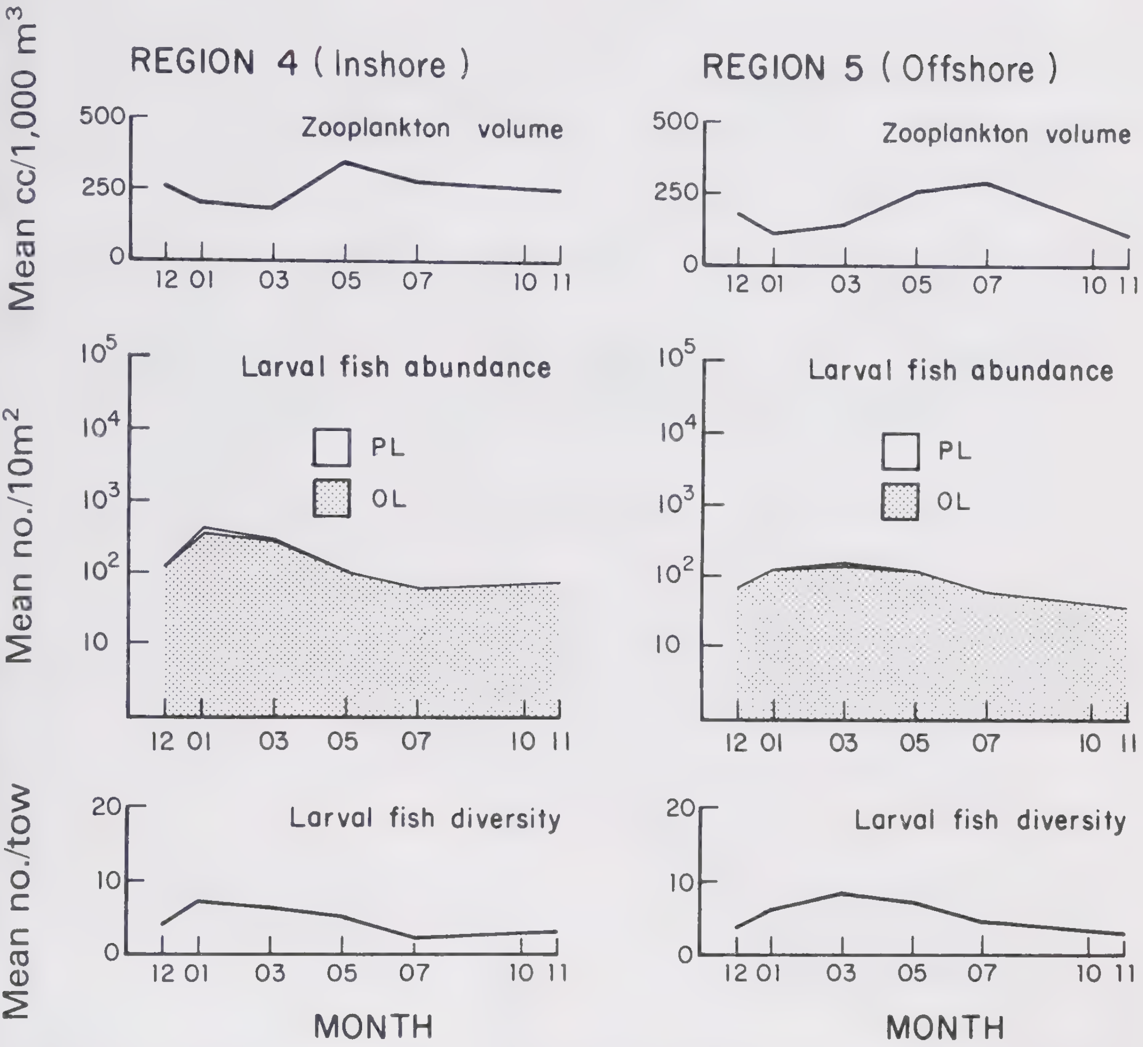

Figure 9. Seasonal variation in zooplankton volume, abundance of fish larvae, and diversity of fish larvae in CalCOFI central California regions 4 and 5 during 1975. Zooplankton biomass expressed as mean displacement volume; abundance of total fish larvae, PL fraction, and OL fraction expressed as mean numbers/10 m^2 sea surface; and larval fish diversity expressed as mean numbers of taxa cruise. Note use of log scale for larval fish abundance.

seaward regions 8 and 9 dominated from January to May, after which the OL made up > 50% of the total. The large January PL abundance of region 8 was due mostly to anchovy and was the highest for the entire CalCOFI area during 1975. Hake larvae made up most of the PL of region 9. In all three regions, larval diversity increased with OL abundance. Significant maximum zooplankton values occurred during March and May in region 7, and May in region 8.

Northern Baja California: regions 11, 12, 13, and 14. The inshore and Viscaino Bay regions 11 and 12 of northern Baja California demonstrated different patterns of seasonal abundance and diversity (Figure 11). Although both regions had January-May periods of maximum PL abundance (anchovy and hake in region 11; primarily anchovy in region 12), maximum OL abundance and diversity occurred during January and March in region 11 and during July in region 12. Overall, the OL in Viscaino Bay region 12 (dominated by flatfishes) made up a larger proportion of the ichthyoplankton (18.6% vs 9%) than in region 11 (primarily rockfishes and mesopelagic fishes). Maximum zoo-

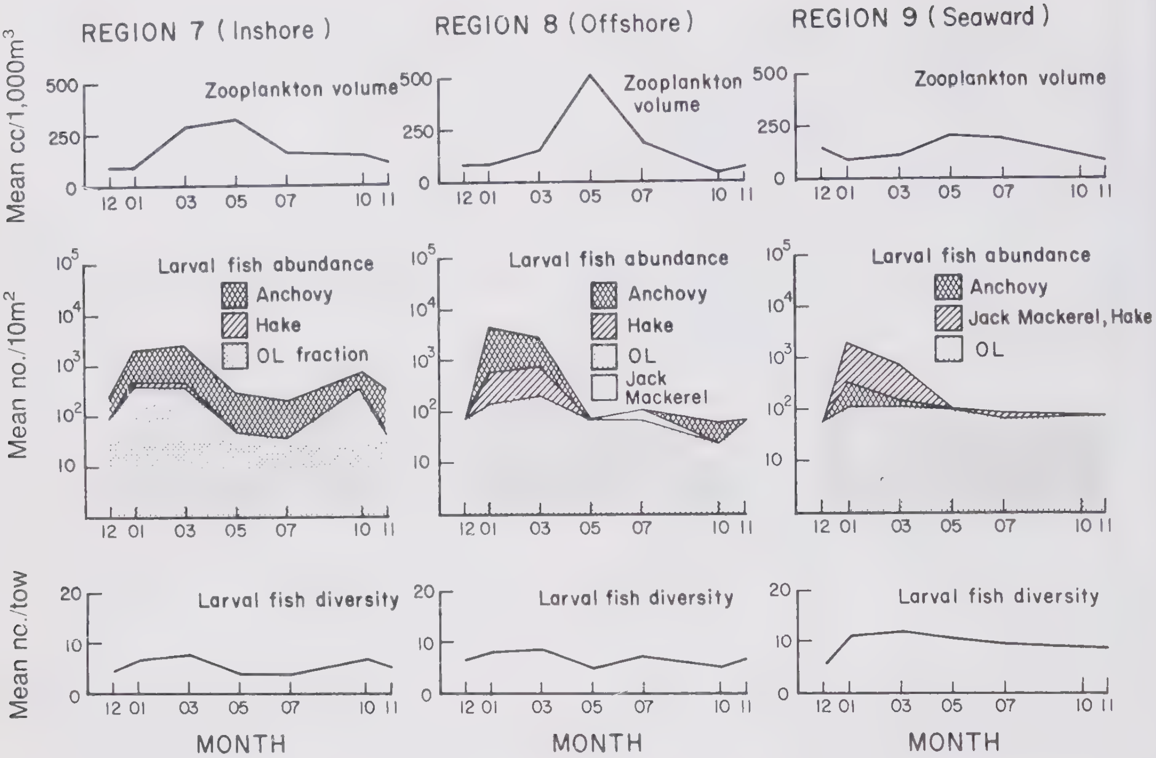

Figure 10. Seasonal variation in zooplankton volume, abundance of fish larvae, and diversity of fish larvae in CalCOFI southern California regions 7, 8, and 9 during 1975. Values as in Figure 9.

plankton biomass values occurred earlier (March) in region 12 than in region 11 (May).

In regions 13 and 14, the PL abundance maximum was shorter (January-March in 13; only March in 14) and less marked than inshore. The January to May PL abundances in both regions were significantly lower than those of regions 11 and 12. Anchovy dominated the January abundance maximum in region 13 (96% of total larvae), but hake and jack mackerel contributed most of the larvae during March (58%); hake and jack mackerel dominated the March peak (67%) in region 14 (Figure 11). OL abundances in region 13 were relatively constant throughout the year. The OL dominated the ichthyoplankton of region 14 during all months but March; lowest abundances occurred in December. Diversity values within region 14 were the highest for the entire CalCOFI area and were relatively constant throughout the year. Zooplankton abundances in both regions were low; a small but significant maximum occurred in region 13 during May.

Central Baja California: regions 16 and 17. Inshore region 16 was unique in having significantly larger numbers of PL during December than any other region (Figure 12); this was primarily due to anchovy (88% of total). Anchovy and PL abundance remained high in January and increased significantly during March. OL abundance was low from December to March and increased significantly in July and October, while PL abundance decreased; the OL made up > 67% of the total ichthyoplankton during July and October. Larval diversity increased in October in conjunction with increased OL abundance. Zooplankton had a significant March abundance peak.

Little can be determined about March and May abundances in offshore region 17 because only five samples represented these months. Based on existing data, this region resembled adjacent region 14, which had peak PL and OL abundances in March and July, respectively (Figure 12). Zooplankton abundances were elevated during March and October.

Chelton (1981) reports that maximum zooplankton biomass values occur in the central Baja California area (regions 16 and 17) during late summer and fall (August-October); this peak is not evidenced here because we lack sample data covering this period.

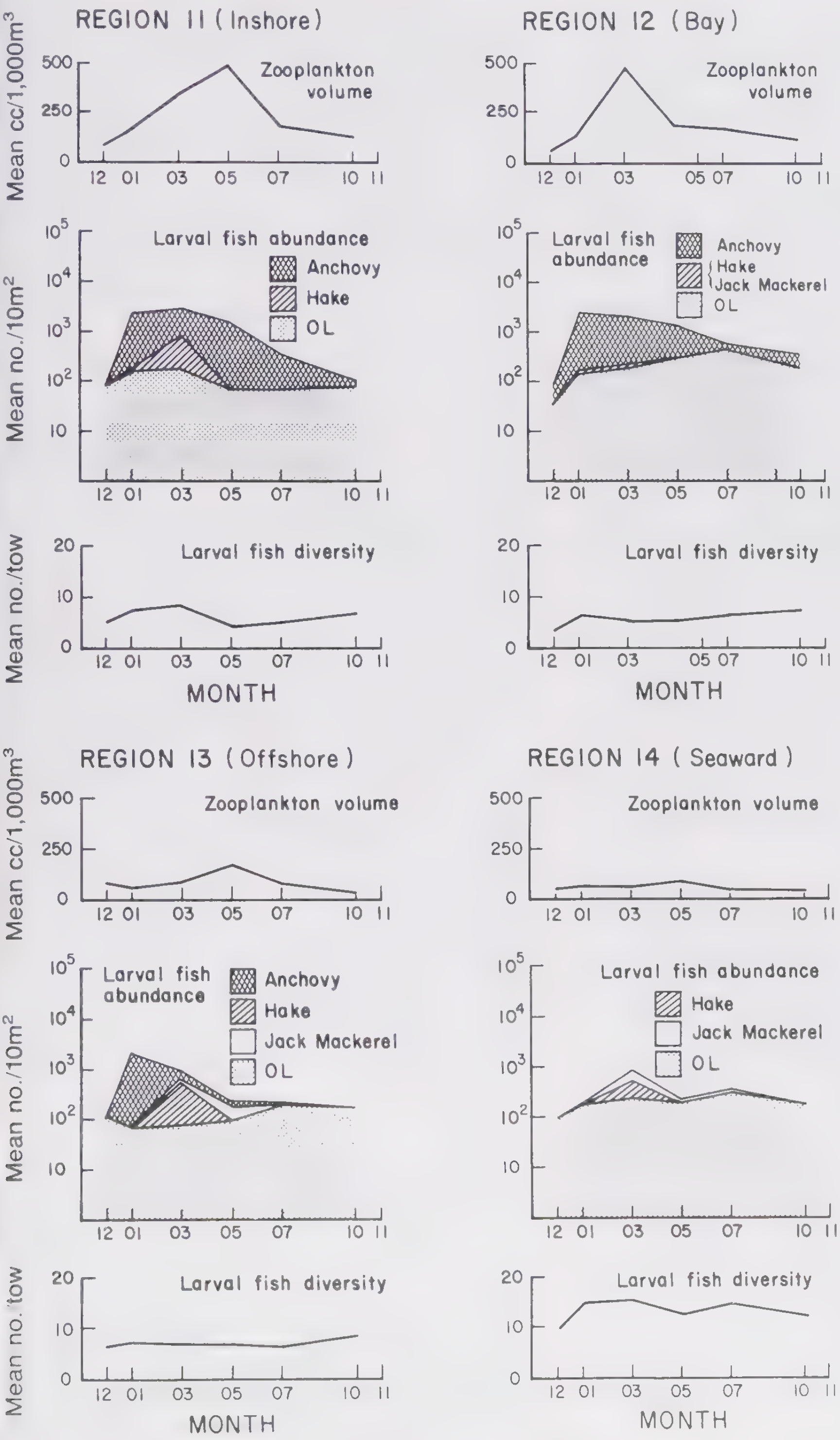

Figure 11. Seasonal variation in zooplankton volume, abundance of fish larvae, and diversity of fish larvae in CalCOFI northern Baja California regions 11, 12, 13, and 14 during 1975. Values as in Figure 9.

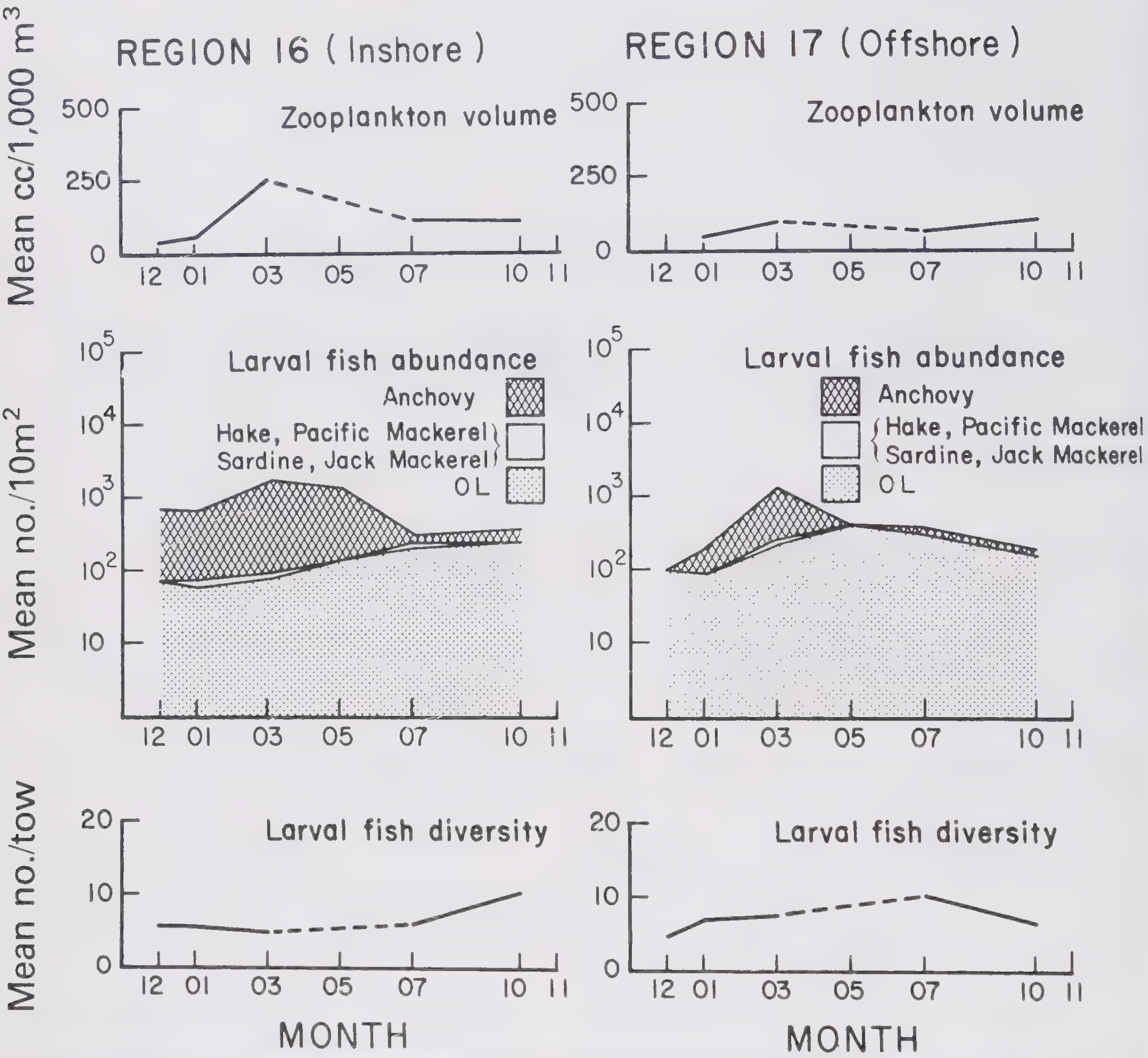

Figure 12. Seasonal variation in zooplankton volume, abundance of fish larvae, and diversity of fish larvae in CalCOFI central Baja California regions 16 and 17 during 1975. Values as in Figure 9.

Sampling Variability, Patchiness, and Abundance Estimates

The large tow-to-tow variability of abundance and resulting large index-of-dispersion values (Table 4) indicate a high degree of zooplankton and ichthyoplankton patchiness throughout the area. Zooplankton biomass index-of-dispersion values during 1975 (range of monthly means 42.8-324.7) were typical for the CalCOFI area and resembled those from years of moderate intensity, coarse-scale (30 × 30 km) patchiness (Haury et al. 1978).

The intensity of zooplankton and ichthyoplankton patchiness varied geographically and seasonally. Within each cruise, zooplankton, total larval, and OL index-of-dispersion values were generally positively correlated with regional abundance values (rank difference correlation coefficients 0.49-0.98; $P \leq 0.05$ in 15/18 cases). However, during all but the December cruise maximum zooplankton index-of-dispersion values (1.2-2 times larger than next highest values) occurred in northern Baja California inshore region 11 and were never associated with maximum regional biomass values. Maximum indices of dispersion for total larvae and OL occurred in northern Baja California Viscaino Bay region 12 during all but the December and January cruises; these were associated with maximum regional abundances of total larvae during May, July, and October and [illegible] OL during May and July. These high index-of-dispersion values indicate generally greater intensities of both zooplankton and ichthyoplankton patchiness and suggest that throughout much of the year the coastal northern Baja California regions were subject to greater physically induced and/or inherent biological heterogeneity than were the other regions in the survey area.

Within each region, maximum zooplankton and OL patch intensities were generally associated with periods of maximum abundance. Greatest PL patch intensities, however, were associated with periods of maximum abundance only in offshore and seaward regions 9, 13, 14, and 17; most intense patchiness preceded maximum PL abundance in inshore regions 7, 11, and 16 by 2 months and followed maximum abundance in offshore region 8 and Viscaino Bay region 12 by 2 and 4 months, respectively. In all cases this was due to anchovy larvae, which exhibited most extreme patch intensity during the onset of spring spawning activity in the inshore regions and at the end of maximum spawning activity in regions 8 and 12. This suggests more localized or erratic anchovy spawning activity prior to or following peak spawning in inshore regions as compared to those offshore.

Despite sampling variability, both seasonal and geographical differences in abundance and diversity were apparent and statistically significant. In contrast, day-night differences in ichthyoplankton abundance estimates were generally nonsignificant statistically and were less than expected (Bridger 1956; Ahlstrom 1959). As a consequence, we combined day and night samples (day and night data are equally represented) for comparisons of relative abundances within and between regions. Absolute abundance estimates based on combined data will be ~ 15% lower than if based on mean night values alone.

Geographical Abundance and Diversity Patterns

The pattern of decreasing zooplankton abundance from north to south and from inshore to offshore regions (Figure 2) has also been reported by Reid et al. (1958), Smith (1971), and Bernal (1980). The pattern of total larval abundance (Figure 3) is heavily influenced by the PL fraction (Figure 5), and resembles distributions of the more abundant pelagic schooling species: anchovy, hake, and jack mackerel (Kramer and Smith 1970a, b; 1971). The southern California and northern Baja California areas of maximum larval abundance coincide with areas of decreased zooplankton abundance and maximum zooplankton diversity (McGowan and Miller 1980). The OL abundance pattern (Figure 6) is complex and includes (1) decreasing abundance from inshore to offshore regions off California, (2) markedly increased abundances in northern Baja California Viscaino Bay and seaward regions, and (3) moderately high inshore and offshore abundances off central Baja California. This complexity is in part due to the large number of species represented in the OL (shelf, benthic, mesopelagic, and oceanic forms with differing hydrographic affiliations and fecundities). These are treated in Loeb et al. (1983a).

The overall zooplankton, PL, and OL abundance patterns differed markedly. There were no significant area-wide correlations between zooplankton biomass and ichthyoplankton abundances (Kendall's tau test: $P > 0.05$ in all comparisons of 6-month mean zooplankton biomass values and abundances of total larvae, PL, and OL). Additionally, no significant correlation was found between 6-month mean PL and OL abundances within regions. This suggests that overall regional patterns of zooplankton, PL, and OL abundances within the CalCOFI area are independent of one another (i.e., that zooplankton, PL, and OL are most abundant within different regions in the CalCOFI area).

The independence of zooplankton, PL, and OL abundances seen between regions on a 6-month basis is also seen within each region (between cruises) on a seasonal scale, and within each cruise on regional scales (30 × 30 km, samples only hours to days apart). Significant within-region differences occur in the timing of abundance fluctuations of the zooplankton, PL, and OL, as indicated by a lack of significant correlations between the ranked mean abundances of these three categories by cruise within each region (Kendall's tau, $P > 0.20$ in all cases). Additionally, there are few significant correlations between zooplankton biomass and ichthyoplankton abundance in samples by region and cruise (product-moment correlation coefficients; Table 8), and there is no overall trend in correlations between regions. This latter strongly suggests independently distributed patches of zooplankton and of larval fish taxa.

In seven regions, periods of peak OL abundances were associated with maximum larval diversity. However, OL abundance and diversity (by cruise) were significantly correlated ($P < 0.05$; Kendall's tau) throughout the year only within regions 4, 5, and 9. In no region was there a significant correlation between diversity and either PL or zooplankton abundance.

TABLE 8

Number of Significant Correlations ($P \leq 0.05$) Out of the Total Number of Within-Region Cruise Comparisons of Zooplankton Biomass (cc/1000m^3) and Abundances (no./10m^2 sea surface) of Four PL Species and the OL Category

Region	Zooplankton vs anchovy	Zooplankton vs hake	Zooplankton vs jack mackerel	Zooplankton vs sardine	Zooplankton vs OL	OL vs anchovy	OL vs hake	OL vs jack mackerel	OL vs sardine
4	0/6	0/4	—	—	2+/6	0/6	0/4	—	—
5	0/2	0/2	0/2	—	1+/6	0/2	0/2	0/2	—
7	0/6	1−/5	0/3	0/2	2+/6	0/6	1+/5	0/3	0/2
8	1+/6	1+/2	0/2	—	2+/6	1+/6 1−/6	0/3	0/2	—
9	3+/4	1+/3	1−/2	—	2+/6 1−/6	0/4	0/2	—	—
11	1+/3	1−/3	0/4	0/1	0/6	3+/4	1+/3	1+/4	0/1
12	1+/3	0/4	1−/3	1+/4 1−/4	1+/6	4+/6	1+/4	0/3	1+/3
13	1+/5	0/4	0/3	—	0/6	1+/5	1−/4	0/3	—
14	0/5	0/2	0/3	—	1+/6	0/5	0/2	1+/3	—
16	1+/5 2−/5	1−/4	0/2	2+/4	3+/5	1+/5	0/4	0/2	0/4
17	2+/4	0/2	0/2	—	1+/5 1−/5	0/4	1−/2	0/2	—
Sum: Positive correlations	10+/49 (20.0%)	2+/35 (5.7%)	—	3+/11 (27.3%)	15+/64 (23.4%)	10+/55 (18.2%)	3+/35 (8.6%)	2+/24 (8.3%)	1+/10 (10.0%)
Negative correlations	2−/49 (4.1%)	3−/35 (8.6%)	2−/26 (7.7%)	1−/11 (9.1%)	2−/64 (3.1%)	1−/55 (1.8%)	2−/35 (5.7%)	—	—

Significance is based on product-moment correlation coefficients derived from $\log_{10}$ abundances of each category within samples by region and cruise.

Seasonal Abundance and Diversity Patterns

Latitudinal differences in timing of peak zooplankton, PL, and OL abundances were tested using Kolmogorov-Smirnov (K-S) tests on cumulative percent curves constructed using summed mean cruise values of the three categories for each area (Figure 13). The cumulative percent curve for zooplankton biomass vs month for the central California area was significantly different ($P < 0.05$) from those of all other areas; that of southern California was significantly different from the northern Baja California (but not central Baja California) area curves; northern and central Baja California area curves did not differ significantly. Maximum differences among those curves occurred between March and May and indicate earlier seasonal zooplankton abundance peaks in the southern areas. Less than 50% of the total central California area zooplankton was captured between January and May, but over 60% of the southern California and central Baja California area zooplankton, and over 70% of the northern Baja California area zooplankton, was captured during this period. Adequate seasonal coverage of the reported (Chelton 1981) late-summer central Baja California zooplankton biomass peak, however, may distinguish this area from the others by establishing the existence of a significantly later zooplankton peak south of Punta Eugenia.

The cumulative percent curves of PL and OL abundance by cruise also showed significant latitudinal differences ($P < 0.05$) except between the OL of the central and southern California areas. For both PL and OL, maximum increases in cumulative percent abundance within southern areas occurred later in the year than in the northern areas (Figure 13). For the PL, the largest differences occurred between January and March; for the OL, the largest differences occurred between March and May. Additionally, within all four areas the cumulative percent curves for zooplankton, PL, and OL abundances were significantly different from one another ($P << 0.01$). This picture of significant differences in timing of zooplankton, PL, and OL abundance peaks is corroborated by lack of significant agreement of ranked abundance (by cruise) of these three categories (Table 9). Only in the northern Baja California area was there significant agreement (Kendall concordance test, $P < 0.05$) among the zooplankton, PL, and OL; abundances were highest in March-July and lowest in October-December.

Significant inshore-offshore differences also occur in the months of PL and OL peak abundances (Figure 14). K-S tests indicate that the timing of PL and OL abundance peaks was similar in the offshore and seaward regions within each area, but (except for the central California area) maximum PL abundances (pri-

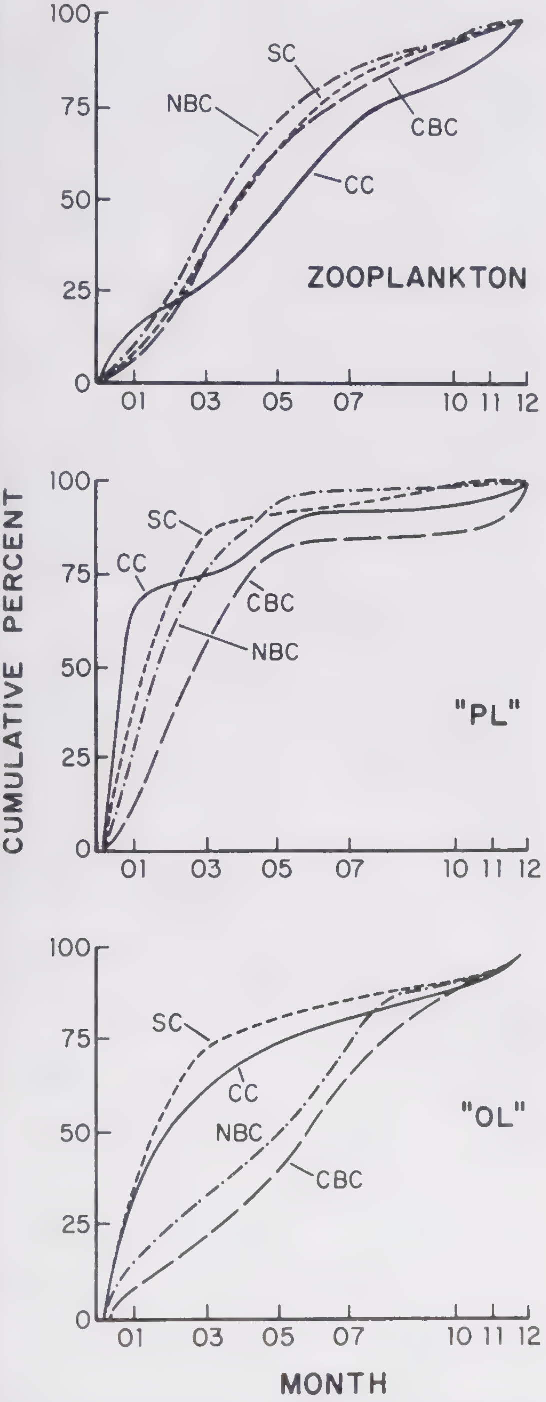

Figure 13. Cumulative percent curves of zooplankton biomass (cc 1000 m^{-3}), PL, and OL abundance (mean no./10 m^2 sea surface) by cruise for four latitudinal CalCOFI areas. CC = Central California; SC = Southern California; NBC = Northern Baja California; CBC = Central Baja California

TABLE 9

Kendall Concordance Test of Abundances of Zooplankton Biomass, PL, and Other Larvae (OL) Ranked by Cruise for Each of Four Latitudinal CalCOFI Areas

	Zooplankton	PL	OL	
Central California				
7412	3	3	3	
7501	5	1	1	
7503	6	4	2	
7505	1	2	4	
7507	2	5	6	
7510(11)	4	6	5	$W = 0.35$ $X_5^2 = 5.29$ $p > 0.05$
Southern California				
7412	6	6	3	
7501	5	2	1	
7503	2	1	2	
7505	1	4	4	
7507	3	5	6	
7510(11)	4	3	5	$W = 0.47$ $X_5^2 = 7.0$ $p > 0.05$
Northern Baja California				
7412	6	5	6	
7501	4	2	4	
7503	1	1	2	
7505	2	3	2	
7507	3	4	1	
7510(11)	5	6	5	$W = 0.77$* $X_5^2 = 11.57$ $p = 0.05$
Central Baja California				
7412	6	4	5	
7501	5	3	6	
7503	1	1	4	
7505	2	2	3	
7507	4	6	1	
7510(11)	3	5	2	$W = 0.41$ $X_5^2 = 6.24$ $p > 0.05$

W is Kendall concordance coefficient value; probabilities are based on X_5^2 values at (n-1) degrees of freedom. Asterisk denotes significant correlation.

marily anchovy) in these regions occurred earlier ($P \leq 0.05$) than in the inshore regions. Zooplankton abundances in offshore and seaward regions lagged (nonsignificantly) behind those of inshore regions.

DISCUSSION

Ichthyoplankton is treated here as an element of the macrozooplankton. Larval fishes are a persistent, albeit relatively rare (McGowan and Miller 1980) zooplankton component, present in varying abundances throughout the year and area. Individuals are, however, only temporary members of the plankton; their residency lasts from hatching to metamorphosis, a period of weeks to months. The importance of larval fishes is not their abundance or competition/predation relations with the macrozooplankton, but how their distribution and abundance relate to adult fish populations, which do have a large collective impact on secondary and fish production in the water column. Fishes are most easily caught in their larval stages. Ichthyoplankton collections from the upper ~200m represent the offspring of a wide variety of fishes

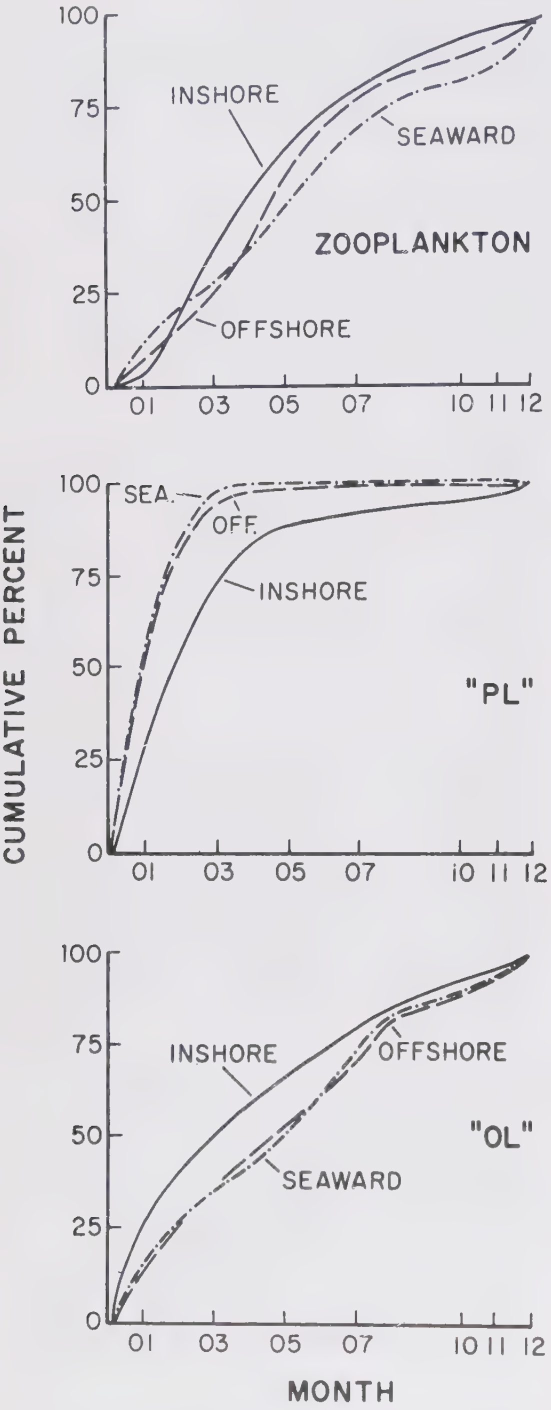

Figure 14. Cumulative percent curves of zooplankton biomass (cc/1000 m^3), PL, and OL abundance (mean no./10 m^2 sea surface) by cruise for inshore, offshore, and seaward CalCOFI zones during 1975.

occurring throughout the water column. Presumably, ichthyoplankton abundance is greatest when and where optimal physical and biological conditions occur for larval survival and ultimate recruitment. Conditions favorable for ichthyoplankton and holoplanktonic invertebrate zooplankton may differ radically, as may conditions favorable for different ichthyoplankton taxa within an area or ichthyoplankton taxa in different areas. These differences should be reflected by different patterns of distribution and abundance between the ichthyoplankton and zooplankton and within the ichthyoplankton.

The geographical and seasonal patterns of zooplankton and ichthyoplankton distribution and abundance described here appear to be related to the physical dynamics of the California Current system. These patterns reflect inshore-offshore and north-south differences in advection and mixing of water from the subarctic, central, and equatorial water masses, and also reflect surface-layer divergence (upwelling) and convergence (downwelling) systems (Reid et al. 1958; Parrish et al. 1981). The differences in distributional patterns and abundance fluctuations of the ichthyoplankton and zooplankton, as well as those of the PL and OL ichthyoplankton categories, suggest that physical processes are influencing these assemblages in different ways. Various patterns of zooplankton and PL distribution and abundance relative to physical processes are discussed below. Patterns within the complex multispecies OL fraction are treated in Loeb et al. (1983a).

The overall pattern of zooplankton abundance (Figure 2) is related to the distribution of surface nutrient levels; maximum abundances are in areas of increased nutrient levels because of advection of subarctic water and coastal upwelled water (Reid et al. 1958). High zooplankton volumes off California are associated with the influence of subarctic water and intense upwelling along the central coastal area extending to Point Conception; high volumes off Baja California are associated with coastal upwelling, especially in the vicinity of Punta Baja and Punta Eugenia (Parrish et al. 1981).

In coastal southern California waters (and presumably elsewhere) the seasonal zooplankton abundance cycle is closely associated with that of primary productivity (Smith and Eppley 1982); both primary productivity and zooplankton biomass increase with the seasonal onset of upwelling in early spring, and reach maximum values during peak upwelling (Smith and Lasker 1978; Smith and Eppley 1982). The zooplankton cycles along the coast (at least from Punta Eugenia northward) appear to follow the northward seasonal progression of coastal upwelling. Off Baja California, upwelling continues throughout the year, with maximum intensities during spring. Off southern and central California, upwelling begins in spring and reaches maximum intensities during summer; upwelling intensities off central California are stronger, and the peak occurs later than off southern California. Chelton (1981) found no significant correlations between zooplankton abundance and upwelling in the four latitudinal CalCOFI areas except off northern Baja California. However, this general lack of correlation may in part result from his use of 30-year averages of monthly biomass and upwelling values; these could obscure existing intra-annual correlations.

Maximum ichthyoplankton abundance (Figure 3) occurs in the coastal regions of southern California and northern Baja California (the Southern California Bight) and is due to large spawning stocks of migratory PL species. This area is characterized by minimal offshore surface water transport relative to the rest of the Pacific coast; Parrish et al. (1981) suggest that PL spawning here may be a reproductive strategy to minimize loss of egg and larval stages to less favorable seaward environments. Anchovy and hake abundances here peak in late winter (January-March), prior to the onset of spring upwelling. For anchovy (and possibly for hake), relatively stable water column conditions at this time may provide well-defined layers and aggregations of larval fish food, and this may favor successful feeding of the early stages (Lasker 1978). Later larval stages grow and develop during periods of upwelling and increasing zooplankton abundance, and actively feeding juvenile stages are contemporary with the May zooplankton abundance peak. The other PL species (jack mackerel, sardine, and Pacific mackerel) have peak spawning during periods of maximum upwelling and increasing zooplankton abundance (March-May); at this time the larval food stocks (copepod nauplii; Arthur 1977) are at their highest.

The persistent high intensity of zooplankton patchiness in northern Baja California region 11 is associated with a persistent zone of surface-layer convergence extending from offshore areas and impinging on the coast between Punta Baja and Punta Eugenia (Nelson 1977; Bakun and Nelson 1977; Parrish et al. 1981). This coastal area is characterized by strong upwelling, and Bakun and Nelson (1977) predicted that surface-layer convergence here may result in the formation of fronts and convergent patches of recently upwelled water. Convergence may also concentrate near-surface zooplankton in fronts or patches (Parrish et al. 1981). The extreme zooplankton patchiness, plus concentrations of characteristically offshore zooplankton species in the inshore northern Baja California region (Arthur 1977) appear to confirm the physical nature of these predictions.

The northern Baja California area of convergence and maximum upwelling separates the cyclonic eddy of the Southern California Bight and a seasonal eddy south of Punta Eugenia (Parrish et al. 1981). It also separates subpopulations of various pelagic fishes (anchovy, hake, sardine, jack mackerel, and Pacific mackerel; Nelson 1977; Hewitt 1981; Parrish et al. 1981) as well as coastal zones of high (northern Baja California) and low (central and southern Baja California) zooplankton diversity (McGowan and Miller 1980). Additionally, the reported late summer/fall zooplankton peak off of central Baja California (south of Punta Eugenia) distinguishes this area from the three northern areas. This late seasonal peak may result from surface expression of the nutrient-rich inshore countercurrent (Reid et al. 1958) and the onset of gyral circulation off the central and southern Baja California coast during the period of relaxed upwelling. These features suggest that the coastal region south of Punta Eugenia represents a separate biological regime (i.e., one with its own species composition and regulating influences).

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APPENDIX

Estimated absolute abundances (as numbers x 10^{11}) of total larvae, PL, and OL fractions of the total, and of the 5 species constituting the PL, by region and cruise. Abundances of total larvae, PL, and OL are ranked by cruise and by region (pooled cruises).

	Region													
Cruise	4	5	7	8	9	11	12	13	14	16	17	Total	Percentage of area total	Cruise rank
7412														
Total	8.08	7.48	14.75	3.44	5.26	5.62	3.40	9.12	10.51	33.21	5.40	106.27	3.70%	6
PL	0.19	0.84	8.62	0.39	—	2.80	2.26	0.32	—	29.62	—	45.04	2.46%	4
OL	7.89	6.64	6.13	3.05	5.26	2.82	1.14	8.80	10.51	3.59	5.40	61.23	9.56%	6
Anchovy	0.13	0.84	8.50	0.39	—	2.80	2.26	0.32	—	29.22	—	44.46		
Hake	0.05	—	0.12	—	—	—	—	—	—	0.03	—	0.20		
Sardine	—	—	—	—	—	—	—	—	—	0.37	—	0.37		
7501														
Total	25.92	12.60	134.09	190.69	186.43	69.21	92.42	151.88	19.13	30.58	15.50	928.45	32.37%	1
PL	2.48	—	107.13	184.42	176.14	64.13	86.75	147.03	2.39	27.81	8.46	806.75	43.89%	1
OL	23.44	12.60	26.96	6.27	10.28	5.08	5.67	4.85	16.74	2.77	7.04	121.70	19.08%	3
Anchovy	0.72	—	100.98	165.91	18.76	63.31	86.43	146.64	2.39	27.12	8.38	620.64		
Hake	1.76	—	6.14	18.51	157.39	0.82	0.05	0.39	—	0.27	0.08	185.41		
Jack mackerel	—	—	0.01	—	—	—	—	—	—	—	—	0.01		
Sardine	—	—	—	—	—	—	0.27	—	—	0.42	—	0.69		
7503														
Total	18.98	14.92	172.11	112.12	65.20	90.60	76.91	67.06	86.49	80.99	100.40	885.78	30.88%	2
PL	0.24	0.17	147.00	103.89	54.20	84.81	69.93	61.54	62.56	77.12	83.24	744.69	40.51%	2
OL	18.74	14.75	25.12	8.23	11.00	5.79	6.98	5.52	23.93	3.87	17.16	141.09	22.11%	1
Anchovy	0.12	0.04	141.27	81.30	1.51	65.11	68.56	22.30	0.25	76.73	82.06	539.25		
Hake	0.12	0.11	5.72	22.59	51.87	19.56	1.32	37.67	29.39	0.28	0.13	168.76		
Jack mackerel	—	0.02	—	—	0.82	0.14	0.05	1.57	32.92	0.12	1.04	36.68		
Sardine	—	—	0.05	—	—	—	—	—	—	—	—	0.05		

						Region								
Cruise	4	5	7	8	9	11	12	13	14	16	17	Total	Percentage of area total	*Cruise rank
7505														
Total	6.30	11.77	20.27	3.15	9.62	44.26	54.99	17.66	21.84	64.52	30.72	285.10	9.94%	3
PL	0.34	1.11	16.77	0.11	0.16	42.16	44.31	9.76	1.11	58.00	—	173.83	9.46%	3
OL	5.96	10.66	3.50	3.04	9.46	2.10	10.68	7.90	20.73	6.52	30.72	111.27	17.44%	4
Anchovy	0.18	—	16.77	0.11	—	41.98	44.05	4.28	0.05	58.00	—	165.42		
Hake	0.16	1.11	0.003	—	0.16	0.01	—	0.07	—	—	—	1.51		
Jack mackerel	—	—	—	—	—	0.17	0.01	5.41	1.06	—	—	6.65		
Sardine	—	—	—	--	--	—	0.25	-	—	-	--	0.25		
7507														
Total	3.81	5.54	13.72	4.91	7.90	10.52	23.33	16.30	33.90	13.91	26.40	160.23	5.59%	4
PL	0.09	0.12	11.33	2.18	1.83	8.43	5.90	2.14	1.75	4.38	2.62	40.77	1.73%	6
OL	3.72	5.41	2.39	2.73	6.07	2.09	17.43	14.16	32.15	9.53	23.77	119.46	20.12%	2
Anchovy	0.09	—	11.29	0.15	0.02	8.34	5.83	1.24	0.01	3.32	2.61	32.90		
Hake	—	—	—	—	—	—	0.06	—	0.02	0.005	-	0.085		
Jack mackerel	—	0.12	0.05	2.03	1.81	0.09	—	0.90	1.72	0.05	0.01	6.78		
Sardine	—	—	—	—	—	—	0.01	—	—	0.99	—	1.00		
7510-11														
Total	4.81	3.17	23.29	2.20	6.72	3.22	13.00	5.69	18.00	16.37	14.03	110.50	3.85%	5
PL	0.005	—	20.31	1.31	0.15	0.76	5.65	0.02	0.08	5.45	2.13	35.87	1.95%	5
OL	4.81	3.17	2.97	0.89	6.57	2.46	7.35	5.67	17.92	10.92	11.90	74.63	11.70%	5
Anchovy	0.005	—	20.20	1.26	0.15	0.73	4.96	—	0.08	5.13	2.13	34.64		
Hake	—	—	0.11	—	—	—	0.006	0.02	—	—	—	0.14		
Jack mackerel	—	—	0.002	0.05	—	0.01	0.002	—	—	—	—	0.06		
Sardine	—	—	0.003	—	—	0.02	0.64	—	—	0.25	—	0.91		
Pac. mackerel	—	—	—	—	—	—	0.04	—	—	0.08	—	0.12		

						Region							
Cruise	4	5	7	8	9	11	12	13	14	16	17	Total	
Grand total for 6 1-month cruises	67.90	55.48	378.23	316.51	281.13	223.43	264.05	267.71	189.87	239.58	192.45	2,476.33 x 10^{11}	larvae
Percentage (total)	2.74%	2.24%	15.27%	12.78%	11.35%	9.02%	10.66%	10.81%	7.67%	9.67%	7.77%		
Regional rank	10	11	1	2	3	7	5	4	9	6	8		
Total PL	3.34	2.24	311.16	292.30	232.49	203.09	214.80	220.80	67.88	202.38	96.46	1,846.94 x 10^{11}	PL
Anchovy	1.24	0.88	299.01	249.12	20.44	182.27	212.09	174.77	2.77	199.52	95.18	1,437.31 x 10^{11}	anchovy
Hake	2.10	1.22	12.13	41.10	209.42	20.39	1.44	38.15	29.41	0.59	0.21	356.16 x 10^{11}	hake
Jack mackerel	—	0.14	0.01	2.08	2.63	0.41	0.06	7.87	35.70	0.17	1.05	50.13 x 10^{11}	jack mackerel
Sardine	—	—	0.008	—	—	0.02	1.17	—	—	0.25	—	3.22 x 10^{11}	sardine
Pac. mackerel	—	—	—	—	—	—	0.04	—	—	0.08	—	0.12 x 10^{11}	Pacific mackerel
Total OL	64.56	53.24	67.07	24.21	48.64	20.34	49.25	46.91	121.97	37.20	95.99	629.39 x 10^{11}	OL
Region													
Percent PL	4.92%	4.03%	79.90%	92.35%	82.70%	91.01%	81.35%	82.48%	35.75%	84.47%	50.12%	Percent PL	74.23%
Percent OL	95.08%	95.97%	20.10%	7.65%	17.30%	8.99%	18.65%	17.52%	64.25%	15.53%	49.88%	Percent OL	25.77%
Regional contribution to													
Total PL	0.18%	0.12%	16.44%	15.90%	12.65%	11.06%	11.68%	12.01%	3.69%	11.01%	5.25%		
Total OL	10.12%	8.34%	11.91%	3.79%	7.62%	3.15%	7.72%	7.35%	19.12%	5.83%	15.04%		
Regional ranked abundance													
PL	10	11	1	2	3	6	5	4	9	7	8		
OL	4	5	3	10	7	11	6	8	1	9	2		

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LOEB ET AL: RECURRENT GROUPS OF LARVAL FISH IN CALIFORNIA CURRENT
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RECURRENT GROUPS OF LARVAL FISH SPECIES IN THE CALIFORNIA CURRENT AREA

VALERIE J. LOEB[1]
San Diego Natural History Museum
P.O. Box 1390
San Diego, California 92112

PAUL E. SMITH AND H. GEOFFREY MOSER
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038

ABSTRACT

Recurrent group analysis was performed on larval fish species collected during the 1975 CalCOFI survey. We arranged 27 species in 11 groups based on frequencies of co-occurrence in samples; 5 other species had "high" affinities with some members of the groups. The 2 largest groups (5 and 4 species, respectively) and their 5 associated species pair groups represented 2 major ichthyoplankton assemblages in the CalCOFI area.

Species of each group were frequently taken together in CalCOFI samples, shared generally similar geographical and seasonal distributions, and appeared to be relatively constant parts of one another's environments. However, based on existing vertical distribution information, most group members and associated group species appear to inhabit different depths within the upper water column. This probably indicates limited interspecific contacts (e.g., competition for food). Within-group differences in timing of peak abundances and, in one case, regions of maximum abundance, also reduce the probability of such interactions. As a result, direct interactions at the larval stage may be negligible in controlling the larval abundances and distributions of these species. More detailed vertical distribution information is needed to verify this observation.

RESUMEN

Se efectuaron análisis de grupos recurrentes con varias especies de larvas de peces recolectadas en 1975 durante las exploraciones del programa CalCOFI. 27 especies se distribuyeron en 11 grupos, tomando como base la frecuencia en que aparecían juntas en las muestras, y otras 5 especies presentaban afinidad elevada con alguno de los integrantes del grupo. Los dos grupos mayores, con 5 y 4 especies respectivamente, así como el grupo incluyendo 5 pares de especies asociadas, representaban dos amplias agregaciones de ictioplancton en la zona explorada.

Especies de cada grupo aparecían juntas frecuentemente en las muestras de CalCOFI, presentando distribuciones similares, tanto en espacio como en época del año, apareciendo como partes constantes de ambos ambientes marinos. Sin embargo, tomando como base la información que existe sobre la distribución batimétrica de las especies, la mayor parte de los integrantes del grupo y las especies asociadas, habitaban al parecer diferentes profundidades en la columna de agua atravesada durante el arrastre de la red. Esto indica que, probablemente existen contactos limitados interespecíficos, por ejemplo, competición por alimento. Diferencias dentro del grupo en cuanto a la època de máxima abundancia y regiones de abundancia máxima, reducen también la probabilidad de tales interrelaciones. Las interacciones a nivel de fase larval pudieran resultar de valor directo insignificante, en cuanto al control de la abundancia de larvas y la distribución de estas especies. No obstante, se precisa obtener más información detallada sobre la distribución batimétrica de las especies para poder comprobar estas observaciones.

INTRODUCTION

The ichthyoplankton of the California Current system contains many disparate members, including the larvae of (1) demersal fishes that spawn on the continental shelf and slope, (2) mesopelagic species whose spawning distributions extend across the Pacific, (3) migratory species that feed in rich boreal and northern temperate waters but enter the area to spawn, (4) subarctic and temperate/tropical species whose spawning ranges extend into the northern and southern regions of the area, and (5) species whose distributions are limited to offshore California Current waters.

In addition to the broad geographic sources of the ichthyoplankton, there is a finer-scale structure to larval fish distribution, on the order of meters to tens of kilometers. Although population breadth prevents delimitation of many species, fine-scale structure may also obscure descriptions of coincidence and possible interaction among species. The fundamental CalCOFI sample is of an oblique column of water 800 m long and only a few meters wide from a depth of 210 m. Consequently, species occurring horizontally within several tens of meters of each other and which could be interacting may not be found in the same samples. Conversely, species coming from widely different depths and which may have minimal interaction may be found in the same integrated sample.

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[1] Current address: Moss Landing Marine Laboratories, P.O. Box 223, Moss Landing, CA 95039

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There are sufficient differences in the biota at different water-column depths to minimize the problem of oblique integrated samples (Gruber et al. 1982). To overcome the problem of using small samples to represent wider, possibly more relevant community units, it is necessary to consider "recurrent groups" of species in many samples. Aggregation (patchiness) of larval fishes appears to be the rule rather than the exception (Loeb et al. 1983a). Thus it is necessary when forming useful recurrent groups to initially disregard the numbers of fishes and consider instead only species presence/absence in each sample. To do otherwise would grant the occasional coincidence of large numbers of two or more species greater importance than its frequency would warrant. Thus interrelationships among group species are not dominated by localized situations favoring the abundance of some or all members. Once groups are established based on significant frequency of co-occurence of all member species in samples, one may consider abundances of individual species. In doing this, one may categorize abundance relationships indicating predator-prey or no apparent interactions, and may explore aspects of concordance among member species as to optimal environmental conditions.

The study of definitive interactions between any two fish species or among any number of species can only be guided by the results of analysis we report here. The sampling grid is too large; the water volume filtered by each sample is too small; and the number of individuals of the proposed interacting species are too few to offer conclusive findings at this stage of analysis. It is the purpose of this paper, therefore, to explore an existing set of CalCOFI data sufficiently that future specific sampling and surveys may be conducted to delineate species interactions in recurrent groups and make substantive inferences about the nature of their interactions.

METHODS

The recurrent group analysis was based on larval fish species presence/absence data from 1,531 standard CalCOFI samples taken on seven cruises between December 1974 and November 1975 (Loeb et al. 1983a). Subsequent analyses of species abundance relations are based on pooled data representing 11 basic CalCOFI regions. Regional and seasonal sampling information is presented in Table 1. Samples were collected using a net of 1 m mouth diameter, fitted with 505-µm mesh, and fished obliquely to ~ 210 m (Kramer et al. 1972).

Recurrent groups analysis was per Fager (1957, 1963). In this analysis an index of affinity (*A*) is calculated between all possible species pairs. This index may range from 0.0 (species pair never caught together) to 1.0 (species pair co-occurred in every sample). It is difficult to assign probability levels to affinity values because the distribution of the affinity values is a function of both the number of occurrences of individual species and the frequency of co-occurrences of paired species. The investigator specifies a significant affinity level (*a*) to be used in developing groups: an *a* level near 1.0 represents a more stringent grouping criterion than does a lower value. A recurrent group is defined as a set of species each of which has a significant affinity level value (i.e., $A \geqslant a$) with every other member of the set. Each group species has affinity values with every nongroup species; some of those values may also be significant. Additionally, a member of one group can have significant affinity values with members of other groups. Selection of a "significant" affinity level is subjective; the subsequent grouping procedure is en-

TABLE 1
Regional Sampling Effort, 1975 CalCOFI Survey

		Cruise/month							
Area	Region	7412 Dec.	7501 Jan.	7503 Mar.	7505 May	7507 July	7510 Oct.	7511 Nov.	Total no. samples
Central California	4	26	26	23	13	24	—	25	137
	5	10	4	18	9	12	—	11	64
Southern California	7	80	81	81	79	77	7	74	479
	8	10	8	9	9	9	4	4	53
	9	18	18	16	18	18	—	14	102
	10	2	2	—	—	—	—	—	4
Northern Baja California	11	26	26	19	27	26	28	—	152
	12	28	28	18	28	28	29	—	159
	13	13	13	10	13	13	12	—	74
	14	4	12	4	12	15	15	—	62
Central Baja California	16	38	38	18	2	37	37	—	170
	17	13	12	4	1	13	13	—	56
	18	—	2	1	2	2	2	—	9

tirely objective. The criterion for selection of a significant affinity value is interpretability of results. In the present study an affinity value $a \geq 0.30$ was used; this is lower than used in many other studies (e.g., Fager and McGowan 1963, $a \geq 0.50$; McGowan and Walker 1979, $a \geq 0.50$; Venrick 1982, $a \geq 0.50$, ≥ 0.65, and ≥ 0.80) primarily because of the low numbers of larval fish taxa taken per sample (Loeb et al. 1983a) and the resulting low numbers of co-occurrences. Intergroup connections are reported as the fraction of possible significant affinities between group member species which actually occurred (i.e., the number of affinities $\geq a/MN$) where M is the number of species in one group and N is the number of species in a second group.

Seventy-eight species were included in the present analysis; higher taxonomic categories and rare species (captured in ≤ 5 samples total) were excluded. We emphasize the largest groups determined and their associated groups; independently distributed species groups and individual group associate species receive only cursory attention. Groups are numbered according to intergroup affinities rather than according to the conventional size-dependent grouping order. Water-mass or hydrographic affiliations are assigned to many of the grouped species. These affiliations are based on the works of Ahlstrom (1965, 1969), Paxton (1967), Moser and Ahlstrom (1970), and Moser et al. (1977).

Three nonparametric statistical tests—Kendall's concordance and tau tests, and rank difference correlation coefficients (Tate and Clelland 1957)—are used to examine regional and seasonal abundance relationships of the grouped species. Kendall's concordance test is a nonparametric analysis of variance used here to examine regional and seasonal abundance ranking across several data sets. The tau and rank difference tests each provide a correlation coefficient that measures the similarity between the order of species abundance rankings within two data sets.

Depth-vs-abundance information for many of the grouped species has been provided by Ahlstrom (1959). Differences between these reported species depth-vs-abundance distributions are tested here using Kolmogorov-Smirnov (K-S) tests (Conover 1971). These tests are based on the maximum differences between cumulative percent curves (here cumulative percent of each species total abundance vs depth curves) for two sets of data.

RESULTS

Species Groupings

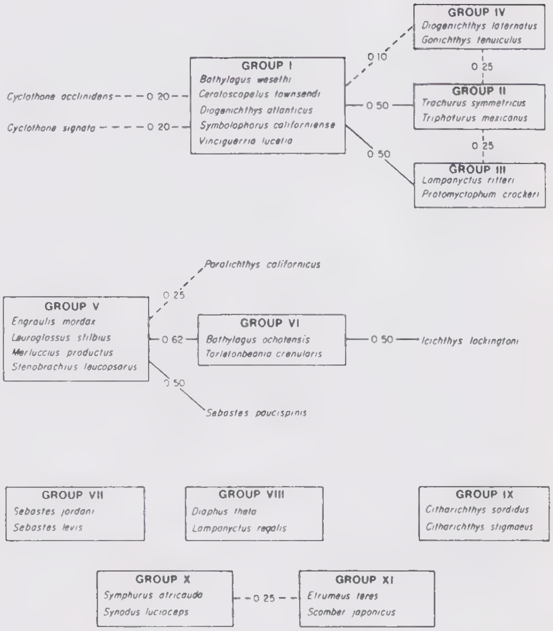

Figure 1. Composition and intergroup affinities of 11 recurrent groups of larval fish species, 1975 CalCOFI survey. Dashed lines denote nonsignificant (< 0.30) intergroup affinity values.

Twenty-seven species formed 11 groups (Figure 1); these included one group of five species (Group I) with three associated species pairs (Groups II, III, and IV); one group of four species (Group V) with one associated species pair (Group VI); and five other species pairs (Groups VII, VIII, IX, X, and XI). Five individual species had affinities ≥ 0.30 with group members. No other species had any affinities ≥ 0.30. The grouped species and group associate species are presented along with their water-mass affiliations in Table 2; within- and between-group affinities are illustrated in Figures 2 and 3.

Group I consisted of five mesopelagic species of mixed hydrographic affiliations: one southern bathylagid; one eastern tropical Pacific gonostomatid; and one each warm-water cosmopolite, restricted California Current, and transition-zone myctophid (Table 2). The four species of Group V included one subarctic-transition zone myctophid, one California Current bathylagid, and the two dominant pelagic species—anchovy (*Engraulis mordax*) and hake (*Merluccius productus*). The nine other groups included three pairs of mesopelagic species (5 myctophids, 1 bathylagid) with northern, subarctic-transition zone, and restricted California Current affiliations (Groups III, VI, and VIII); a California Current myctophid and a pelagic species, jack mackerel (*Trachurus symmetricus*) (Group II); a pair of eastern tropical Pacific myctophids (Group IV); a pair of northern rockfishes (VII); a pair of

TABLE 2
Species Composition of Recurrent Groups and the Water Mass or Habitat Affiliations of Member Species

Group no.	Species name	Affiliation	Group associate species	Affiliation
I	*Diogenichthys atlanticus*	C		
	Bathylagus wesethi	S		
	Symbolophorus californiense	T		
	Vinciguerria lucetia	ETP	*Cyclothone acclinidens*	S
	Ceratoscopelus townsendi	CA	*Cyclothone signata*	S
II	*Triphoturus mexicanus*	CA		
	Trachurus symmetricus	PL		
III	*Protomyctophum crockeri*	CA		
	Lampanyctus ritteri	S-T		
IV	*Diogenichthys laternatus*	ETP		
	Gonichthys tenuiculus	ETP		
V	*Leuroglossus stilbius*	N	*Sebastes paucispinis*	N
	Stenobrachius leucopsarus	S-T		
	Engraulis mordax	PL	*Paralichthys californicus*	M
	Merluccius productus	PL		
VI	*Tarletonbeania crenularis*	S-T	*Icichthys lockingtoni*	M
	Bathylagus ochotensis	N		
VII	*Sebastes jordani*	N		
	S. levis	N		
VIII	*Lampanyctus regalis*	S-T		
	Diaphus theta	S-T		
IX	*Citharichthys sordidus*	N		
	C. stigmaeus	N		
X	*Symphurus atricauda*	M		
	Synodus lucioceps	M		
XI	*Etrumeus teres*	M		
	Scomber japonicus	M		

S-T, subarctic-transition zone; T, transition zone; C, warm-water cosmopolite; ETP, eastern tropical Pacific; N, northern or cold water; S, southern or warm water; CA, restricted California Current; PL, pelagic; M, multiple affiliations. Affiliations based on Ahlstrom (1965), Moser and Ahlstrom (1970), Moser et al. (1977), and Paxton (1967).

northern flatfishes (IX); and two pairs of the comparatively rare larvae of southern coastal and pelagic species (X and XI) (Table 2).

The two largest groups (I and V) had connections with several of the smaller groups (Figure 1). Some of the Group I species had high affinities with members of Groups II and III. Three other mesopelagic species (two individual group associate species and one species from Group IV) each had affinities > 0.30 with one of the Group I species (Figure 1). Group II was also weakly associated (one of four possible significant affinities) with both Groups III and IV. Some of the four Group V member species had high affinities with both Group VI species. One and two of the Group V species were also associated with one flatfish and one rockfish species, respectively. Group VI also had a single-species associate. Only two of the five other species pairs had intergroup affiliations; these were weakly associated (intergroup connection = 0.25) Groups X and XI.

Within Group I, affinity levels ranged from 0.323 to 0.478; highest values (0.439-0.478) occurred between *Diogenichthys atlanticus, Symbolophorus califor-*

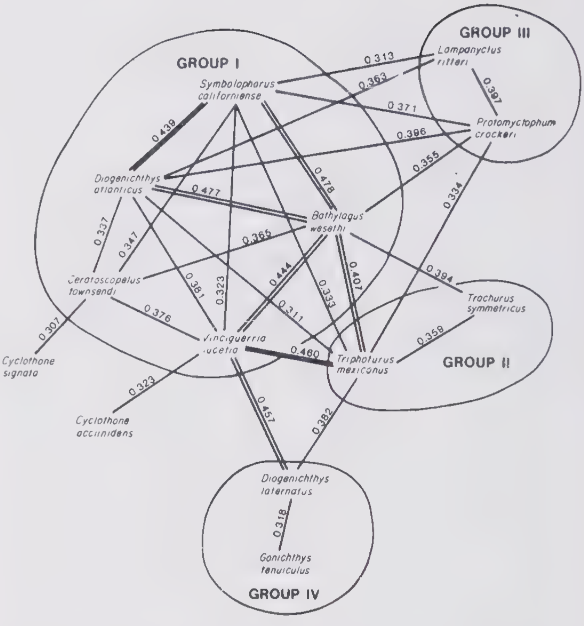

Figure 2. Within- and between-group species affinity values for recurrent Group I and associated Groups II, III, and IV, CalCOFI survey, 1975. Double lines denote species affinity values 0.40-0.49; single lines, affinity values 0.30-0.39

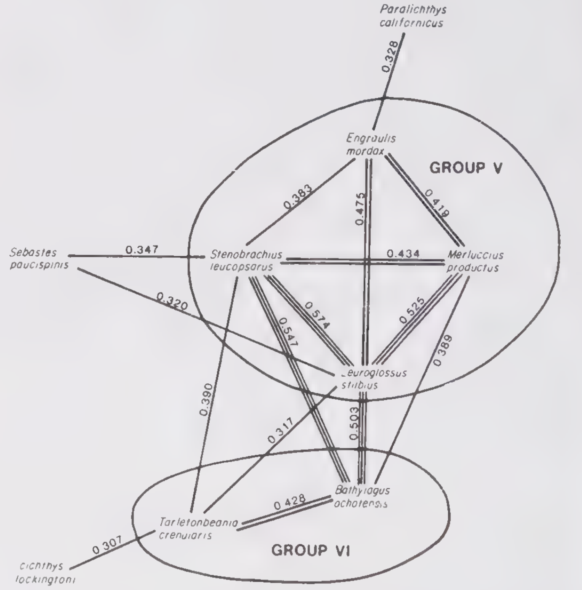

Figure 3. Within- and between-group species affinity values for recurrent Group V and associated Group VI, CalCOFI survey, 1975. Triple lines denote species affinity values ≥ 0.50; double lines, affinity values 0.40-0.49; single lines, affinity values 0.30-0.39.

niense, and *Bathylagus wesethi* and between *Bathylagus wesethi* and *Vinciguerria lucetia* (Figure 2). These four species all had affinities > 0.30 with *Triphoturus mexicanus* of Group II; three of the four (*D. atlanticus*, *S. californiense*, and *B. wesethi*) also had significant affinities (0.313-0.396) with *Lampanyctus ritteri* and/or *Protomyctophum crockeri* of Group III. Additionally, *V. lucetia* had a high affinity (0.457) with Group IV species *Diogenichthys laternatus*. The fifth Group I species, *Ceratoscopelus townsendi*, had relatively low affinities (0.337-0.376) with the other member species, and affinities < 0.30 with members of the three associated groups. Group II species *T. mexicanus*, in addition to its associations with Group I members, also had significant affinities with *D. laternatus* (Group IV) and *P. crockeri* (Group III).

The affinity values between the four Group V species (0.383-0.574) were generally higher than between the Group I species (Figure 3). Highest values occurred between *Leuroglossus stilbius* and hake (*Merluccius productus*) (0.525) and between *L. stilbius* and *Stenobrachius leucopsarus* (0.574). *Leuroglossus stilbius* and *S. leucopsarus* also had high affinity values with Group VI species *Bathylagus ochotensis* (0.503-0.547) and *Tarletonbeania crenularis* (0.317-0.390); hake had an affinity > 0.30 only with *B. ochotensis*, and anchovy (*Engraulis mordax*) had affinities < 0.30 with both species. Both *S. leucopsarus* and *L. stilbius* were also associated with *Sebastes paucispinis*.

Group Distribution and Abundance Relationships

The five Group I species were widely distributed within the CalCOFI area; each was captured in all regions except 4 and 7 (inshore central and southern California) and during all cruises. Co-occurrence in samples by all five species was restricted, however, to offshore and seaward regions 9, 13, and 14 of southern California and northern Baja California; four of the five species also co-occurred in samples within offshore central California and central Baja California regions 5 and 17 (Figure 4). Highest frequencies of co-occurrence were in northern Baja California seaward region 14, where the five species were caught together in 17.7% of all samples; four of five species were caught together in an additional 30.6% of the samples within this region (Table 3). Members of Group I had abundance peaks in the same regions (Kendall's concordance, $P < 0.01$). The regions of maximum abundance (9, 13, and 14) were those of maximum frequency of occurrence of the individual species (rank difference correlation coefficient = 0.85-0.95; $P < 0.01$ in all cases) and of maximum frequency of co-occurrence of the five species (Tables 3, 4). Within regions 9, 13, and 14 there was significant agreement of species rank order of abundance throughout the year (i.e., similar species rankings across all cruises within each region; Kendall's concordance, $P < 0.05$). However, species rankings differed between regions (Table 5), and there was no overall agreement of regional rank order of abundance (Ken-

TABLE 3
Regional Distribution of Six Main Recurrent Groups of Larval Fish Species Based on Frequency of Co-occurrence in Samples by Group Member Species

Area	Central California		Southern California			Northern Baja California				Southern Baja California	
Region	4 (inshore)	5 (offshore)	7 (inshore)	8 (offshore)	9 (seaward)	11 (inshore)	12 (bay)	13 (offshore)	14 (seaward)	16 (inshore)	17 (offshore)
Group I											
5 spp	—	—	—	—	2.0%	—	—	4.0%	17.7%	—	—
					(3)			(2)	(1)		
4/5 spp	—	1.6%	—	—	7.8%	—	—	6.8%	30.6%	—	1.8%
	—	(5)	—	—	(2)	—	—	(3)	(1)	—	(4)
Group II											
2 spp	—	—	0.2%	3.8%	5.9%	11.2%	0.6%	25.7%	40.3%	2.4%	5.4%
	—	—	(9)	(6)	(4)	(3)	(8)	(2)	(1)	(7)	(5)
Group III											
2 spp	1.5%	10.9%	0.8%	11.3%	25.5%	7.9%	3.8%	17.6%	32.2%	0.6%	—
	(8)	(5)	(9)	(4)	(2)	(6)	(7)	(3)	(1)	(10)	—
Group IV											
2 spp	—	—	—	—	—	0.6%	—	—	—	2.4%	23.2%
	—	—	—	—	—	(3)	—	—	—	(2)	(1)
Group V											
4 spp	2.9%	0.2%	13.4%	13.2%	9.8%	2.6%	—	—	1.6%	—	—
	(4)	(7)	(1)	(2)	(3)	(5)	—	—	(6)	—	—
Group VI											
2 spp	24.8%	35.9%	2.5%	17.0%	28.4%	—	—	—	—	—	—
	(3)	(1)	(5)	(4)	(2)	—	—	—	—	—	—

Frequency of co-occurrence presented as the percentage of all samples taken within each CalCOFI region containing all member species. For Group I frequency of co-occurrence is also provided for 4 of the 5 member species. Regional values are ranked for each group (in parentheses).

TABLE 4
CalCOFI Regions Ranked by Abundance for Member Species of Six Main Recurrent Groups of Larval Fish Species

Area	Central California		Southern California			Northern Baja California				Southern Baja California	
Region	4 (inshore)	5 (offshore)	7 (inshore)	8 (offshore)	9 (seaward)	11 (inshore)	12 (bay)	13 (offshore)	14 (seaward)	16 (inshore)	17 (offshore)
Group I											
Bathylagus wesethi	—	9	10	4	3	7	8	2	1	6	5
Ceratoscopelus townsendi	—	8	9	4	3	7	10	2	1	5	6
Diogenichthys atlanticus	11	5	10	8	2	7	6	3	1	9	4
Symbolophorus californiense	—	6	10	5	2	4	7	3	1	9	8
Vinciguerria lucetia	—	9	—	8	7	5	6	3	1	4	2
Group II											
Trachurus symmetricus	—	9	10	3	4	6	8	2	1	7	5
Triphoturus mexicanus	—	—	9	7	8	5	6	3	1	4	2
Group III											
Lampanyctus ritteri	9	6	10	5	3	2	7	4	1	11	8
Protomyctophum crockeri	7	5	9	3	4	6	8	2	1	11	10
Group IV											
Diogenichthys laternatus	—	—	7	—	—	6	4	5	3	2	1
Gonichthys tenuiculus	—	—	—	—	—	—	4	3	—	2	1
Group V											
Engraulis mordax	10	11	4	1	8	3	2	6	9	5	7
Leuroglossus stilbius	3	6	1	2	5	4	9	8	10	7	11
Merluccius productus	8	9	6	2	1	3	7	4	5	10	11
Stenobrachius leucopsarus	1	2	3	5	4	7	—	—	6	8	—
Group VI											
Bathylagus ochotensis	1	2	5	3	4	7	9	6	8	—	—
Tarletonbeania crenularis	1	2	5	3	4	7	—	—	6	—	—

Regional abundance estimates (mean abundances, pooled cruises) from Loeb et al. (1983b).

TABLE 5
Relative Abundances of Group Member Species Within Regions of Species Co-occurrence in Samples, for Six Main Recurrent Groups of Larval Fish

Area	Central California		Southern California			Northern Baja California				Southern Baja California	
Region	4 (inshore)	5 (offshore)	7 (inshore)	8 (offshore)	9 (seaward)	11 (inshore)	12 (bay)	13 (offshore)	14 (seaward)	16 (inshore)	17 (offshore)
Group I											
Bathylagus wesethi	—	3	—	—	1	—	—	2	2	—	2
Ceratoscopelus townsendi	—	4	—	—	4	—	—	5	5	—	4
Diogenichthys atlanticus	—	1	—	—	2	—	—	3	3	—	3
Symbolophorus californiense	—	2	—	—	3	—	—	4	4	—	5
Vinciguerria lucetia	—	5	—	—	5	—	—	1	1	—	1
Group II											
Trachurus symmetricus	—	—	2	1	1	2	2	2	1	2	2
Triphoturus mexicanus	—	—	1	2	2	1	1	1	2	1	1
Group III											
Lampanyctus ritteri	2	2	2	2	2	2	2	2	2	2	—
Protomyctophum crockeri	1	1	1	1	1	1	1	1	1	1	—
Group IV											
Diogenichthys laternatus	—	—	—	—	—	—	1	—	—	1	1
Gonichthys tenuiculus	—	—	—	—	—	—	2	—	—	2	2
Group V											
Engraulis mordax	4	4	1	1	2	1	—	—	2	—	—
Leuroglossus stilbius	2	2	2	3	4	3	—	—	4	—	—
Merluccius productus	3	3	3	2	1	2	—	—	1	—	—
Stenobrachius leucopsarus	1	1	4	4	3	4	—	—	3	—	—
Group VI											
Bathylagus ochotensis	1	1	1	1	1	—	—	—	—	—	—
Tarletonbeania crenularis	2	2	2	2	2	—	—	—	—	—	—

Ranked abundances based on pooled samples (all cruises) within each region (from Loeb et al. 1983b).

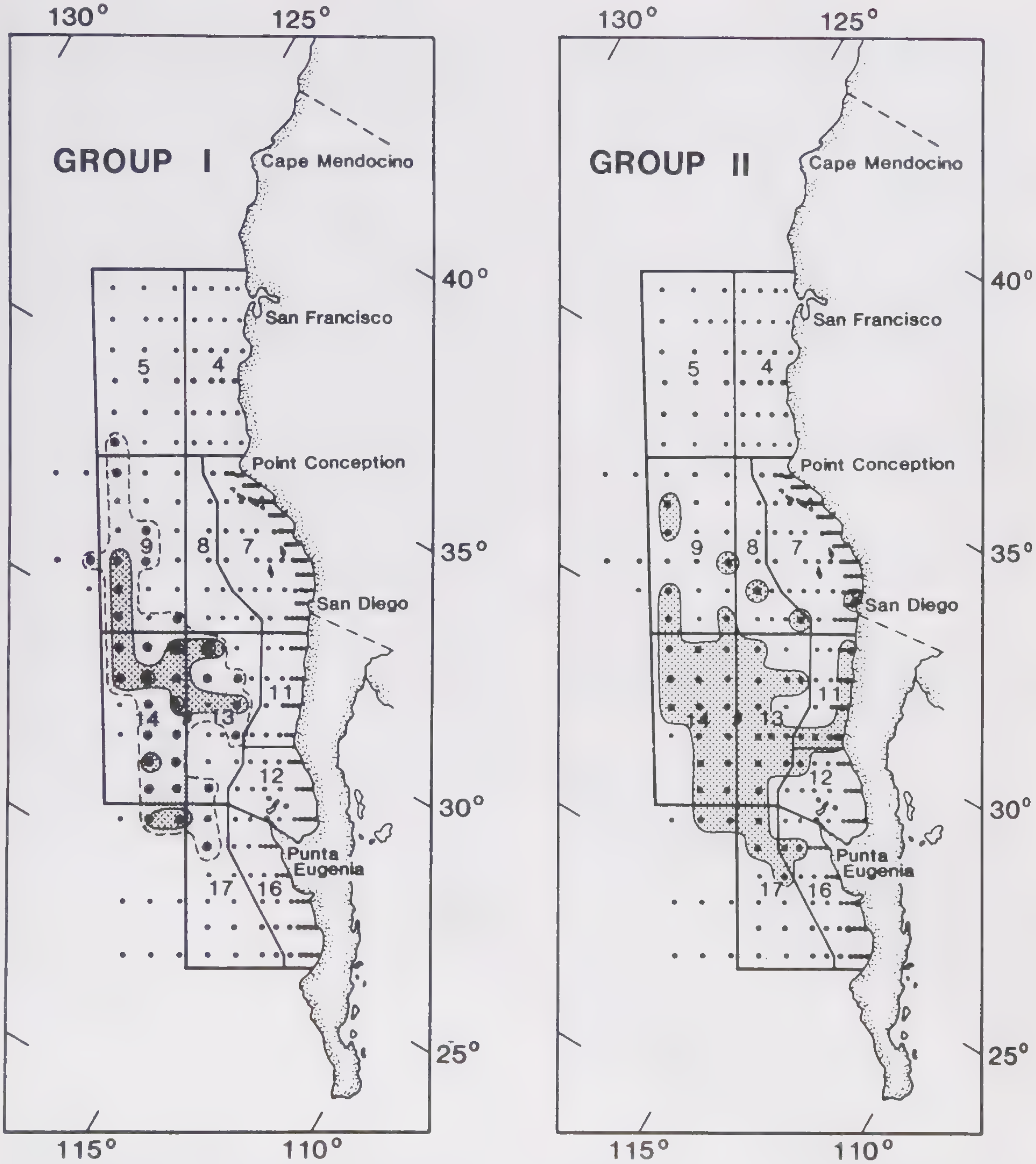

Figure 4. Geographical distributions of recurrent Group I and recurrent Group II in 1975 CalCOFI survey. Station locations are provided for co-occurrences of all five (dark stippling) and four of five (light stippling) Group I species and for both Group II species

dall's concordance, $P < 0.05$). This is directly due to *Vinciguerria lucetia*'s dominance in southern regions 13, 14, and 17 and its rarity in northern regions 5 and 9; significant agreement of rank order of abundance ($P < 0.01$) exists among the four other species. There was no agreement on season of maximum abundance among the member species (Kendall's concordance, $P > 0.05$). *Diogenichthys atlanticus, Bathylagus*

TABLE 6
Cruises Ranked According to Abundances of Member Species of Six Main Recurrent Groups of Larval Fish Species

	Cruise					
	7412	7501	7503	7505	7507	7510
Group I						
Bathylagus wesethi	6	5	1	3	2	4
Ceratoscopelus townsendi	5	4	3	6	2	1
Diogenichthys atlanticus	3	2	1	5	6	4
Symbolophorus californiense	6	3	1	4	2	5
Vinciguerria lucetia	3	4	6	5	1	2
Group II						
Trachurus symmetricus	6	5	1	3	2	4
Triphoturus mexicanus	6	5	4	2	1	3
Group III						
Lampanyctus ritteri	5	1	2	4	3	6
Protomyctophum crockeri	3	1	2	4	5	6
Group IV						
Diogenichthys laternatus	4	3	1	6	2	5
Gonichthys tenuiculus	1	3	5.5	5.5	2	4
Group V						
Engraulis mordax	4	1	2	3	6	5
Leuroglossus stilbius	3	1	2	4	5	6
Merluccius productus	4	1	2	3	5	6
Stenobrachius leucopsarus	4	2	1	3	5	6
Group VI						
Bathylagus ochotensis	4	1	2	3	5	6
Turletonbeania crenularis	6	5	4	2	3	1

Ranks based on cruise abundance estimates (pooled regions) presented in Loeb et al. (1983b).

wesethi, and *Symbolophorus californiense* had March abundance peaks; *Vinciguerria lucetia* and *Ceratoscopelus townsendi* were most abundant in July and October (Table 6).

The Group III member species (*Protomyctophum crockeri* and *Lampanyctus ritteri*) co-occurred throughout the CalCOFI area (Figure 5; Table 3), but their association throughout the year (all 6 cruises) was limited to offshore and seaward southern California and northern Baja California regions 9, 13, and 14. Maximum frequencies of co-occurrence were in northern Baja California region 14 (32% of all samples) and southern California region 9 (25% of all samples) (Table 3). The two species had significant concordance of abundance across regions (Kendall's tau test, $P < 0.01$), and both were most abundant in region 14 (Table 4). Both species had January-March abundance peaks (Table 6). In most regions and cruises *P. crockeri* was more abundant than *L. ritteri* (Table 5).

Group II species (*Trachurus symmetricus* and *Triphoturus mexicanus*) had a more restricted geographical and seasonal distribution than did Group III. There were few co-occurrences of the two species north of Baja California (Figure 4; Table 3); *T. symmetricus* was absent from December samples and was very rare in January samples (Table 6). The two species co-occurred most frequently from March to July in northern Baja California regions 11, 13, and 14 (Table 3), with maximum co-occurrences in seaward region 14 during April (83% of all samples) and July (93% of samples). They showed significant agreement as to regions of maximum abundance (13 and 14; Kendall's tau, $P < 0.01$). Peak abundances of *T. symmetricus* were in March, of *T. mexicanus*, in July (Table 6). Their relative abundances varied with region (Table 5) and cruise.

Group IV (*Diogenichthys laternatus* and *Gonichthys tenuiculus*) was the most geographically restricted group (Figure 5; Table 3). Co-occurrence was limited to southern regions, primarily central Baja California regions 16 and 17. Maximum frequency of co-occurrence and maximum abundances of both species were in region 17 during December and July; these maxima may be artifacts caused by undersampling of regions 16 and 17 during March and May (Table 1). *Diogenichthys laternatus* was consistently more abundant than *G. tenuiculus* (Table 5).

Co-occurrence of all four Group V species was primarily within the regions of central and southern California (Figure 6) and was limited to winter and spring. Highest frequencies of co-occurrence were within southern California regions 7, 8, and 9 during January and March, when all four species were captured together in from 25%-56% of the samples. The four species had different regions of maximum abundance and of frequency of occurrence (Kendall's concordance, $P > 0.05$ in both cases). *Engraulis mordax* (anchovy) was most abundant and frequent in offshore southern California region 8 and inshore northern Baja California regions 11 and 12; *Merluccius productus* (hake) in southern California offshore and seaward regions 8 and 9; *Stenobrachius leucopsarus* in southern California inshore and offshore regions 7 and 8; and *Leuroglossus stilbius* in central California inshore and offshore regions 4 and 5 (Table 4). Although species rank order of abundances within each region were somewhat consistent between cruises, there was no overall between-region agreement (Kendall's concordance, $P > 0.05$; Table 5). All four species had abundance peaks during January-March, and minimum abundances in July and October/November (Kendall's concordance, $P < 0.01$; Table 6).

Group VI was distributed within the five regions of central and southern California (Figure 6). In contrast to associated Group V, the member species of Group VI co-occurred throughout the year in their regions of maximum abundance (4, 5, and 8) (Table 4). *Bathylagus ochotensis* was overall the more abundant species (Table 5), but because of differing periods of peak abundance (Table 5; January-March for *B. ochotensis*, July-November for *Tarletonbeania crenularis*), species abundance relations within regions changed seasonally.

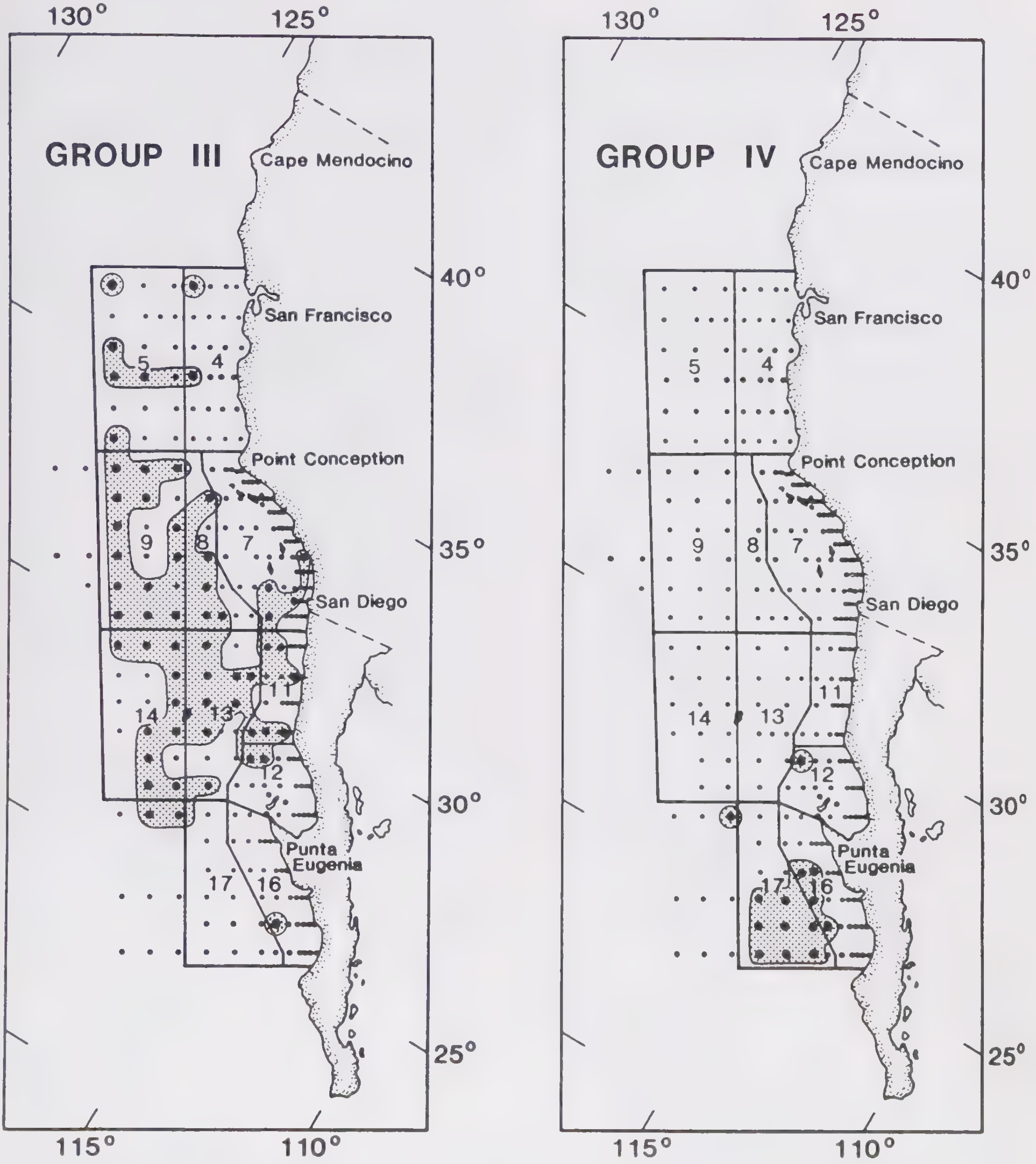

Figure 5. Geographical distributions of recurrent Group III and recurrent Group IV in 1975 CalCOFI survey. Station locations are provided for co-occurrences of both Group III species and both Group IV species.

DISCUSSION

The species forming the major groups (I and V) and their associated groups (II, III, IV, and VI) were the more abundant and widespread species in the CalCOFI area (Loeb et al. 1983b). The species composition of Groups I and V and their associated groups is in general agreement with the two subjectively determined species assemblages described in Loeb et al. 1983b

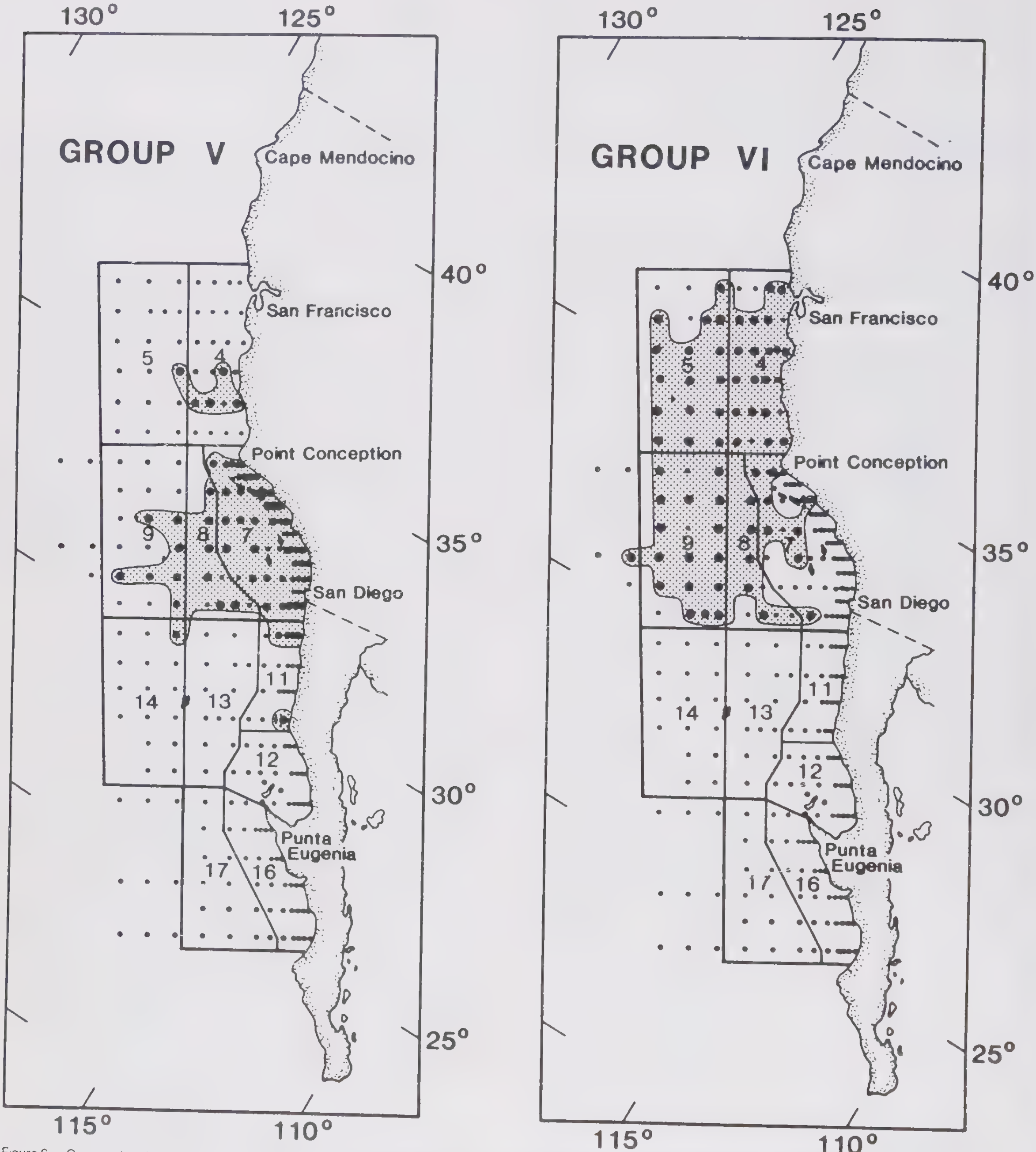

Figure 6. Geographical distributions of recurrent Group V and recurrent Group VI in 1975 CalCOFI survey. Station locations are provided for co-occurrences of all four Group V species and both Group VI species.

(i.e., species with mixed but predominantly warm-water affiliations and highest abundances in northern and central Baja California areas, and species with subarctic-transition zone or northern cold-water affiliations and highest abundances in central and southern California areas). This is probably due to the fact that in all cases the frequency of occurrence of group member species was significantly correlated with their abundance (rank difference correlation coefficients = 0.72-0.96; $P \leq 0.05$ in all cases). However, the objectively formed species groups (based on frequency of co-occurrence rather than on agreement of mean regional abundances) had more restricted geographical distributions (Figures 4-6) than did the subjectively determined assemblages. Group I and associated Group II and III members (predominantly warm-water mesopelagic species) were most frequent in the offshore and seaward regions of southern California and northern Baja California; associated Group IV species (eastern tropical Pacific forms) were restricted to central Baja California regions. Group V (anchovy, hake, and cold-water mesopelagic species) co-occurred most frequently in the southern California regions, and is quite similar to Southern California Bight Group I reported by Gruber et al. (1982); associated Group VI (cold-water mesopelagic species) was most frequent in the regions of central California and the offshore region of southern California.

The groups differed in constancy of species rank order of abundance. Although the members of Group III had widespread distributions, they had similar species rank order of abundance within their regions of maximum frequency of occurrence and between all regions within their distributional range. Group VI was less widely distributed, but also demonstrated between-region constancy. In contrast, Groups I and V had within-region similarity of species rank order of abundance across cruises but had significant between-region differences; Group II had significant differences in species abundance relations both within and between regions. The variability of rank order of abundance within Groups II and V may be related to seasonal and geographical differences in abundances of pelagic schooling species (anchovy and hake in Group V; jack mackerel in Group II). Marked between- and within-region differences in the relative abundances of the two Group V mesopelagic species, however, indicates that variability within this group was not restricted to the pelagic species. Group V variability may be partially due to greater heterogeneity and range of environmental conditions (i.e., coastal vs offshore differences) within the group's range. The geographical variability of rank order of abundance of Group I is primarily due to the northern distributional limit of one member species (*Vinciguerria lucetia*); the other four species have relatively constant abundance relations.

Environments of the Recurrent Groups

Recurrent group analysis identifies groups of species, based on co-occurrence in samples, which are likely to be frequent parts of one another's environment. Groups might then be investigated with respect to interspecific relationships of possible importance in controlling the distribution and abundances of the component species. Interspecific relations such as competition for limited food resources may be extremely important in the survival of larval fishes and their ultimate recruitment to adult populations. The groups identified here were based on geographical and seasonal co-occurrence. Because the data were derived from open oblique plankton tows in the upper ~ 200 m, we do not know if the group member larvae were in fact frequent parts of one another's immediate environments or were separated either vertically or horizontally. Larval depth vs abundance distributions of some of the species of the six major groups are available (Ahlstrom 1959), and are presented here as cumulative percent vs depth curves.

The curves for 8 of the 11 species of Group I and associated Groups II, III, and IV (Figure 7A) and for 5 of the 6 species of Group V and associated Group VI (Figure 7B) show a wide variety of depth-abundance distributions. Within Group I, two species (*D. atlanticus* and *S. californiense*) had similar distributions (K-S test, $P > 0.05$); most of these larvae occurred below those of *V. lucetia* and above those of *B. wesethi* ($P < 0.01$ in all four curve comparisons). The depth vs abundance distributions of the two Group II species also differed significantly ($P < 0.01$); most of the *T. symmetricus* larvae occurred above the *T. mexicanus* larvae. Additionally, only four of the total 21 intergroup comparisons showed similar species distributions. *Trachurus symmetricus* (Group II) had the shallowest distribution of the eight species considered (Figure 7A); this distribution resembled only that of *V. lucetia* (Group I) ($P > 0.05$). The distributions of *T. mexicanus* (Group II) and *L. ritteri* (Group III) were also relatively shallow and similar to each other and to *V. lucetia* (Group I) ($P > 0.05$ in all cases), but significantly different from those of the other four species. The species with deepest distributions—*D. laternatus* (Group IV) and *B. wesethi* (Group I)—were significantly different from each other and from all other species in the Group I and associated group assemblage ($P < 0.01$ in all cases).

The vertical distributions of the four Group V species (Figure 7B) differed significantly ($P < 0.05$). Associated Group VI species *T. crenularis* had a relatively shallow distribution similar to that of Group V species *S. leucopsarus* ($P > 0.05$); most *T. crenularis* larvae were significantly deeper than those of *E. mordax* (anchovy; $P < 0.01$) and shallower than those of *M. productus* (hake) and *L. stilbius* ($P < 0.01$).

It appears likely that although group members were frequently collected within the same locales and seasons they were probably not constant members of each

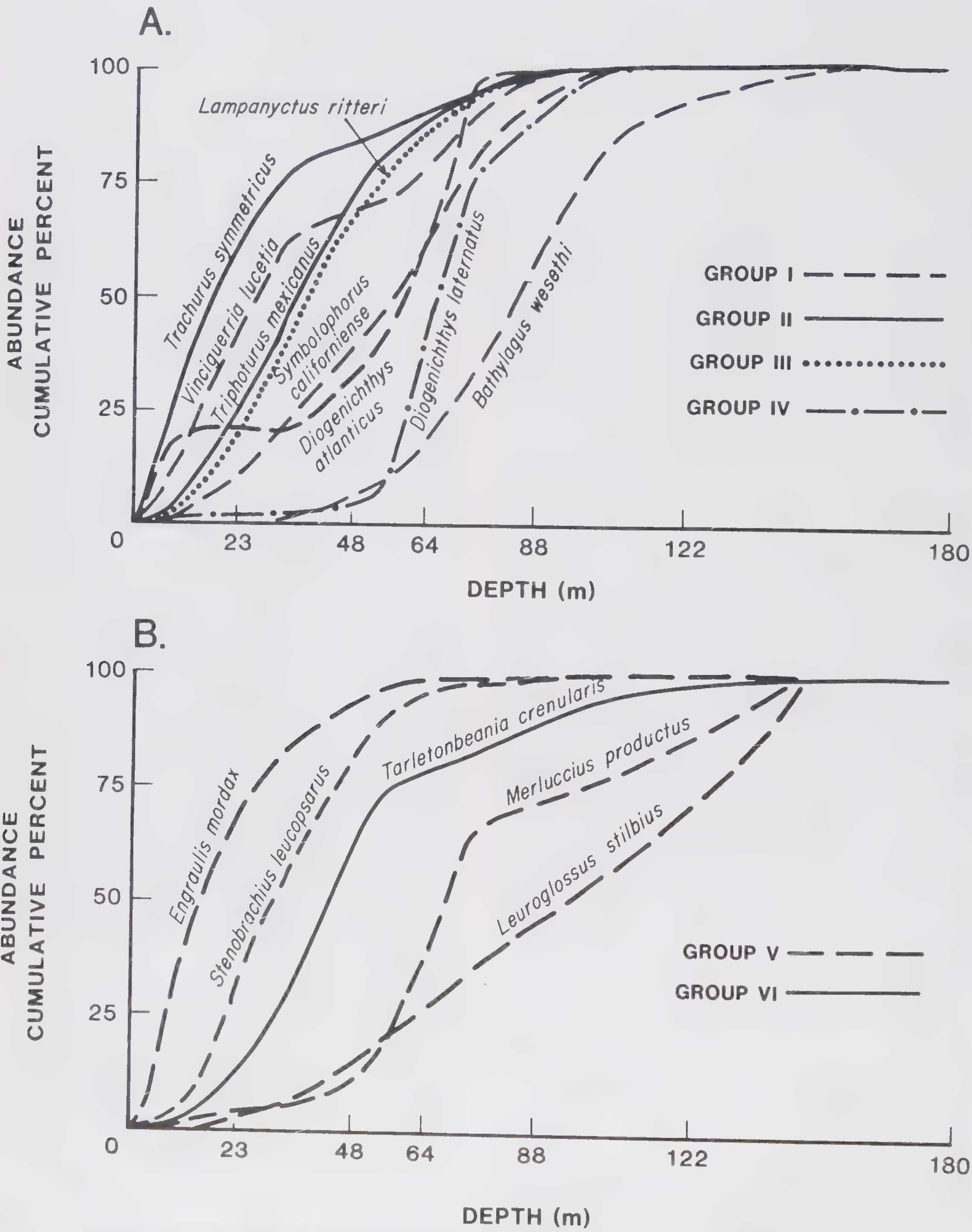

Figure 7 Cumulative percent curves of larval fish species abundance vs depth for (*A*) four Group I species and four species from associated Groups II, III, and IV and (*B*) four Group V species and one associated Group VI species. Vertical abundance distributions from Ahlstrom (1959)

other's immediate environment (except for *D. atlanticus* and *S. californiense* of Group I) because of significantly different depth distributions. Also the group member species generally were not frequent parts of the immediate environments of species from associated groups.

In addition to vertical separation, there were seasonal abundance differences to further reduce the potential impact of interspecific relations within a group. The periods of peak abundances of two of the five Group I species differed from the others; peak abundance periods of both species within the Group II, IV, and VI species pairs differed significantly from each other; and timing of peak abundance of one of the four Group V species differed from the rest. Within Group V, the regions of maximum abundance of the member species differed, thereby further reducing the potential for interspecies impacts.

Because of within-group differences of seasonal, vertical, and (for Group V) geographical distributions, it is probable that, within each group, ecologically important interactions such as direct competition for limited food resources are minimal. This indicates that (based on the present data) within the CalCOFI area such interspecific processes during the larval stages are likely to be negligible in controlling fish species abundances and distributions. However, more detailed vertical distribution information is definitely needed to verify this observation.

ACKNOWLEDGMENTS

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GEOPHYSICAL RESEARCH LETTERS, VOL. 10, NO. 11, PAGES 1093-1095, NOVEMBER 1983

THE 1982-83 WARM EPISODE IN THE CALIFORNIA CURRENT

Ronald J. Lynn

National Oceanic and Atmospheric Administration, National Marine Fisheries Service,
Southwest Fisheries Center, P. O. Box 271, La Jolla, California 92038

Abstract. The Warm Episode (El Niño) of 1982-83 has produced elevated steric height (geopotential anomaly) along the coast of California and Baja California. Fifty percent of the stations observed during a survey in February and March had the greatest steric height observed for this season for the entire 33 years of California Cooperative Oceanic Fisheries Investigations (CalCOFI) observations. Where it occurred onshore, along central California in early February, this anomalous height was balanced by a strong countercurrent. Along Baja California in late March the greatest steric height was offshore and hence produced a strong equatorward flow. These conditions may not have been synoptic. An offshore shift in the subsurface thermal anomaly between January and May suggests a reversal of the flow within this time frame

Introduction

During the winter of 1982-83, high levels of geopotential anomaly (hereafter called steric height) were observed at hydrographic stations off California and Baja California. Steric height, derived from the pressure integral of the specific volume, is the quantity whose lateral gradient is proportional to velocity under the geostrophic assumption. The values given here are for the surface relative to 500 decibars (5MPa) indicated by "0/500 db" and are in the units dynamic cm (10^3 cm^2 sec^{-2}). In one survey during February and March 1983, by the NOAA vessel Townsend Cromwell, conductivity/temperature/depth (CTD) casts were made at stations in the California Cooperative Oceanic Fisheries Investigations (CalCOFI) grid (see e.g. Wyllie, 1966). Of 38 CTD casts which could be compared to the CalCOFI data files, 18 have 0/500 db steric height, which match or exceed long-term records of steric height for each station for this season. The steric height for 11 stations exceed the long-term records for any season. These high levels are commensurate with the large and persistent positive temperature anomaly and the greatly thickened surface mixed layer that has characterized the North American coastal manifestation of the 1982-83 Warm Episode (El Niño) in the Pacific Ocean.

The global-scale climatic fluctuations leading to this Warm Episode were first noted in a Climate Analysis Center bulletin issued 20 September 1982. The large-scale warming in the equatorial zone and along the coast of Peru was fully developed by October 1982 (Rasmusson et al., 1983). Full development of large-scale warming off the North American coast from Mexico to Alaska followed in January 1983 (Auer, 1982, 1983)

Discussion

The physical and biological effects of the El Niño phenomenon upon California waters was central to the presentations at the June 1958 CalCOFI Symposium on "The Changing Pacific Ocean in 1957 and 1958" (Sette and Isaacs, 1960). The 1957-58 El Niño was a strong and well documented event. In the Symposium Proceedings Reid noted that in January 1958 there was, on the average, a 5 dynamic cm steric rise in sea level in the CalCOFI area as a result of both higher temperatures and an increase in thickness of the mixed layer. Stewart (same proceedings) found as much as a 12 cm anomaly in sea level (averaged by months but uncorrected for inverse barometric effects) for the same month at coastal tide stations along California. (There is very nearly a one-to-one correspondence between changes in sea level (cm) and in steric height (dynamic cm).

The large-scale mean distribution of steric height in the North Pacific shows a decrease from mid-ocean toward the California coast, in balance with equatorward flow of the eastern limb of the North Pacific anticyclonic gyre. In winter there is a trough in steric height 40 miles off the California coast and a secondary peak nearshore in balance with the winter coastal countercurrent (Wyllie, 1966). By spring the trough has moved shoreward and the average surface flow is everywhere equatorward along California and Baja California.

In February and March 1983, the high values in steric level along the California coast, north of the middle of the California Bight, exceeded 94 dynamic cm; the highest for these stations in the 33-year CalCOFI record (Figure 1). The high values continued southward in the form of a ridge offshore northern Baja California. The geostrophic flow relative to 500 db for this pattern of steric height is strongly poleward at Pt. Conception and north (20 cm/sec), equatorward south of San Diego (20 cm/sec), and

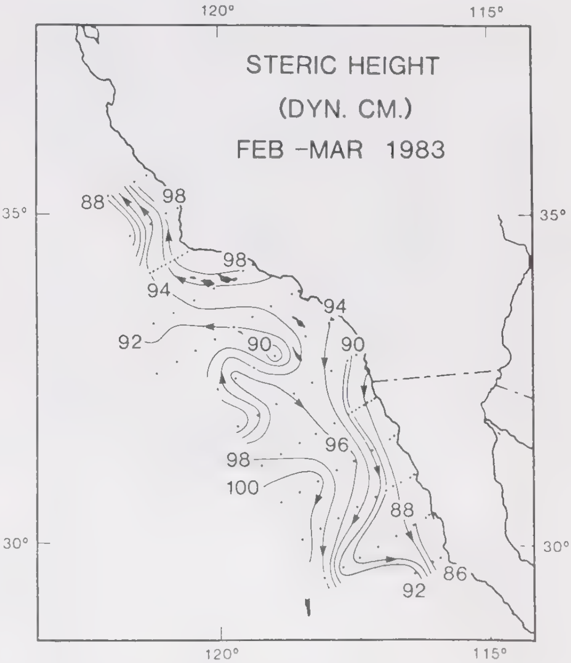

Fig. 1. Steric height 0/500 db in dynamic centimeters for R/V Townsend Cromwell survey 8302-3. The northern four lines were taken in early February, the southern six in late March and the remainder in the intermediate period

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shoreward along much of the outer station grid, especially at the latitude of the U.S./Mexican border (14 cm/sec).

The anomaly of steric height (Figure 2) is produced by subtracting the seasonal mean from the observed values of Figure 1. Except for two stations off central Baja California, steric height was found to be above seasonal values in this El Niño period. The gain is seen to be in excess of 14 dynamic cm off central California and the pattern of anomaly greater than 10 dynamic cm follows the ridge in steric height offshore Baja California. Also, sea level, as measured at local tide stations, has attained new record levels (D. Brown, personal communication). At the Scripps pier station mean monthly tides were 22 and 16 cm above long-term averages for November and December 1982 (Simpson, 1983).

Time Variation in Steric Height

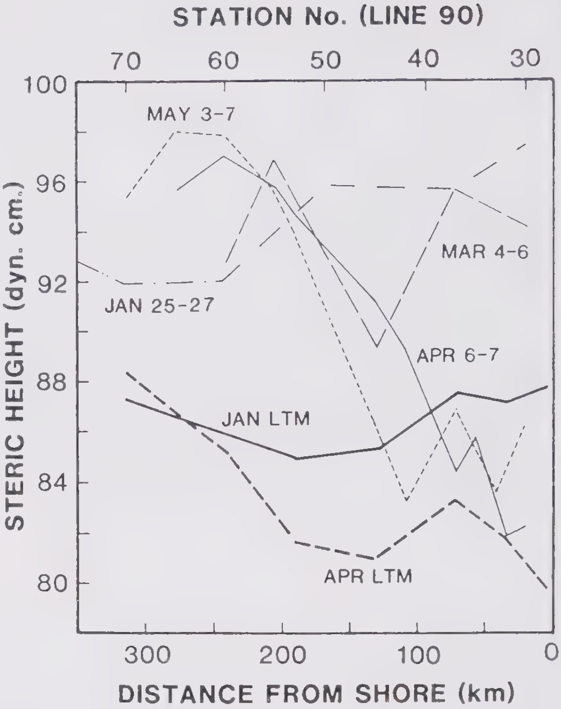

Fig. 3. Steric height along CalCOFI station line 90 for surveys in January, March, April and May 1983 and the long-term mean values for January and April from Lynn et al. (1982).

CTD casts along CalCOFI line 90 have been repeated intermittently during 1983 to monitor conditions associated with the El Niño. Observations were made in late January and early March by the NOAA vessel Townsend Cromwell, in early April by the R/V Wecoma and in early May by the NOAA vessel David Starr Jordan. The steric heights from these surveys (Figure 3) show a continuing excess over the seasonal mean values west of the Channel Islands (outside of 200 km from shore) but within 100 km of the coast, steric height dropped to near the seasonal average after early March. This sequence of observations of steric height implies a reversal of current at that section during March. These changes are commensurate with the displacement of the high values (>3°C) in subsurface temperature anomaly near 75 m from nearshore stations in January to offshore stations in early May (Figure 4). The observations for early March in Figure 4 show a split in the high values with the maximum 200 km offshore and a secondary peak at the nearshore station. In Figures 1 and 2 the four northern lines of stations were taken in the first half of February; the southern six were taken in the latter half of March. It is possible that the ridge in anomalous steric height depicted in Figure 1 may have moved from a coastal position to an offshore position during the 8 weeks spanning the survey. Thus, the distributions given in Figures 1 and 2 probably do not provide a synoptic representation of conditions.

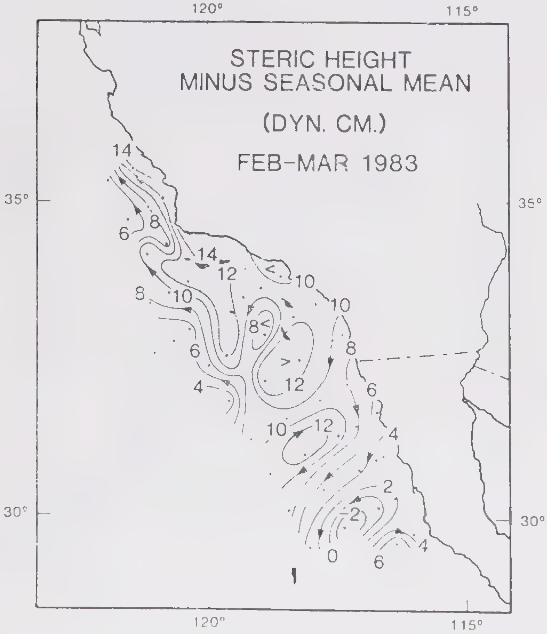

Fig. 2. The difference between the steric height values of Fig. 1 and the seasonal mean values in dynamic centimeters.

There is also a circulation reversal along the coast in February and March in the mean seasonal trend where the cessation of the coastal countercurrent is followed by the establishment of equatorward flow. Although sea surface temperatures along the coast from Baja California to Alaska have been about 1 to 2 C higher than normal during the 1982-83 winter and spring, the temperatures decreased 1°C between early February and early March in a narrow band along this coast, possibly indicating a change to southward advection. Additionally, fishermen claim that there was a dramatic reversal from northward flow to southward flow off northern California in April; both flows were strong enough to interfere with trawling operations.

The 1957-58 El Niño

The differences in steric height for surveys in 1958 from the long-term monthly mean (Figure 5) show a spatially and temporally coherent pattern (Lynn and Reid, 1975). The January anomaly was more than 4 dynamic cm within a 100 km coastal band from Pt. Conception to the southern tip of Baja California. There is a trough in the pattern 350 km offshore where values fell below the monthly mean. These differences show that the California Countercurrent was intensified and broadened during the peak period of the 1957-58 El Niño. The California Current was displaced farther offshore and intensified in a narrow band about its core. The subsequent cruises of April, July and October 1958 show a dimunition, reversal and reestablishment of

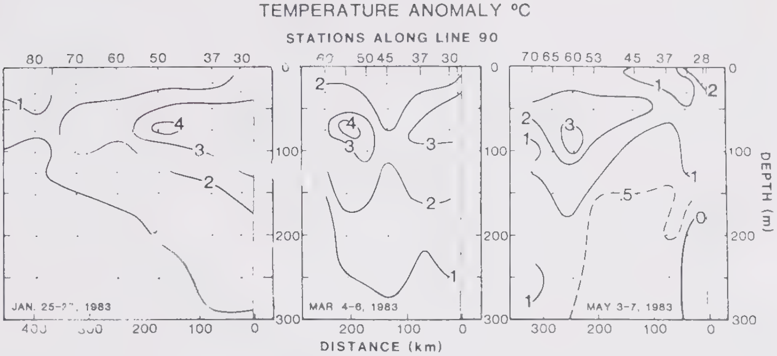

Fig. 4. Vertical sections of temperature anomaly along CalCOFI station line 90 for three periods in 1983 (°C).

the initial anomaly pattern, respectively (Figure 5). Throughout the period there were regions that exceeded a positive anomaly of 8 dynamic cm. Sea surface temperatures were also anomalously high with the greater temperature anomalies generally coincident with the greater steric height anomalies. Negative temperature anomalies were found only in the July survey: these coincident with the negative steric height anomalies. It is yet to be seen whether a similar oscillation of El Niño conditions will also characterize the present event.

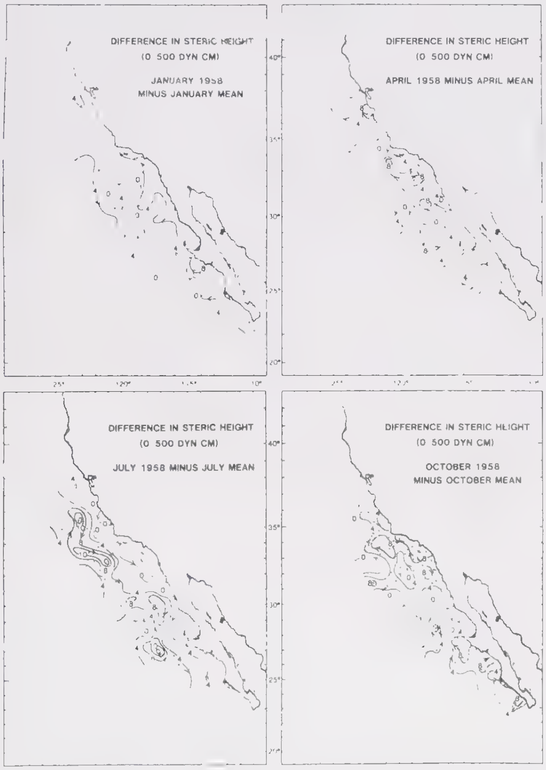
DIFFERENCE IN STERIC HEIGHT (0 500 DYN CM) JANUARY 1958 MINUS JANUARY MEAN
DIFFERENCE IN STERIC HEIGHT (0 500 DYN CM) APRIL 1958 MINUS APRIL MEAN
DIFFERENCE IN STERIC HEIGHT (0 500 DYN CM) JULY 1958 MINUS JULY MEAN
DIFFERENCE IN STERIC HEIGHT (0 500 DYN CM) OCTOBER 1958 MINUS OCTOBER MEAN

Fig. 5. The difference in steric height (0/500 db) from season mean values for four months in 1958 in dynamic centimeters. Values above 4 dynamic centimeters are shaded.

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EASTERN CENTRAL PACIFIC - PACIFICO CENTRO-ORIENTAL

VARIABILITY OF PELAGIC FISH STOCKS OFF CALIFORNIA

by

Alec D. MacCall

National Marine Fisheries Service
Southwest Fisheries Center
P.O. Box 271, La Jolla, California
U.S.A. 92038

Resumen

Los stocks de peces pelágicos costeros de California muestran una variedad de patrones de fluctuación. Los stocks de sardinas del Pacífico se redujeron drásticamente por la excesiva presión de pesca, y su recuperación ha sido lenta. Algún tiempo después de la reducción de la sardina, la anchoveta aumentó, alcanzando aparentemente una abundancia de equilibrio a mediados de los años 1960. Tanto California como México han desarrollado pesquerías de reducción de anchoveta, y el stock está ahora plenamente explotado. El stock de caballa fue reducido a mediados de los años 1960. Pero ahora se ha ido rehabilitando debido a un reclutamiento favorable y a una explotación estrictamente controlada, y en estos momentos sostienen una pesquería saludable. El jurel es un recurso grande y prácticamente no explotado a excepción de una pequeña pesquería en las áreas de cría frente a la parte sur de California. El bonito del Pacífico es una población marginal que recientemente se ha establecido en las aguas al sur de California y su permanencia es cuestionable. El recurso de barracuda de California también está reducido, pero la composición por edades está respondiéndo favorablemente a una limitación del tamaño mínimo de pesca. El estado del robalo blanco de mar es poco claro, pero el recurso está posiblemente sobreexplotado.

La variabilidad de los recursos de peces pueden generarse por muchas causas. Las fluctuaciones del reclutamiento son partícularmente importantes para especies de vida corta. El reemplazamiento de especies parece ocurrir, pero es favorecido o ocurre a través de cambios ambientales. Contrario a las asunciones estándar, los cambios en la tasa de mortalidad natural pueden ser una causa importante de las fluctuaciones en abundancia.

INTRODUCTION

This paper is divided into two sections: the first reviews historical fluctuations in abundance of several pelagic fishes and larger predatory fishes off California. The second section examines assorted pieces of evidence relating to mechanisms causing those fluctuations.

HISTORICAL REVIEWS

Pelagic fishes

California Sardine *Sardinops sagax caerulea*

Population analyses by Murphy (1966) and MacCall (1979) document the history of the Pacific sardine stock (here termed the California sardine to avoid confusion). When plotted on a logarithmic scale (Figure 1), the decline in abundance appears as a coherent trend extending over the entire thirty years of the historical fishery. There are no discontinuities which could be interpreted as adverse environmental changes. Rather, the sustained rate of decline (average instantaneous rate of increase is approximately -0.2/yr) suggests that the fishery consistently exceeded sustainable yields by about 18 percent.

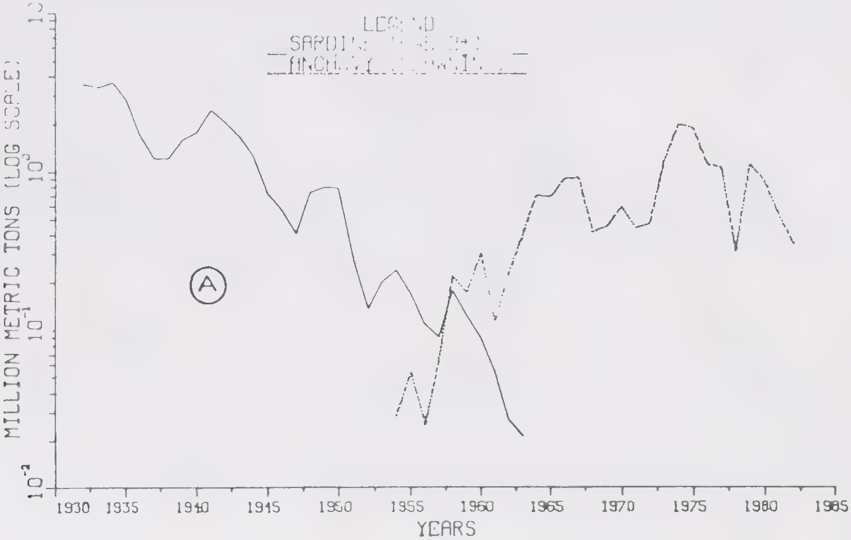

Figure 1. Time series of sardine (age 2+) and anchovy spawning biomass (log scale) off California and northern Baja California. "A" denotes approximate anchovy spawning biomass in 1940-41 (interpreted from Smith 1972).

Exploitation continued until 1970, when a moratorium on sardine landings was enacted by the State of California. During the following decade the resource remained at nearly undetectable levels, and showed no signs of recovery until 1980, when sardines became increasingly frequent as incidental catches in landings of other pelagic fishes. Abundance has increased noticeably as of 1982. A 1982 pelagic fish survey captured sardines in 14 midwater trawl tows, whereas sardines had occurred in only three other tows in the entire previous 20 years of surveys (Mais 1982). A small fishery will be allowed when the stock reaches a biomass of 20,000 tons, which is a possibility in the near future.

Northern Anchovy *Engraulis mordax*

Understanding of northern anchovy population fluctuations has been revolutionized by recent development of an "egg production method" of biomass estimation (see Parker 1980, Picquelle and Hewitt 1983 in press). Previous population estimates based on larva abundance have been insensitive to changes in true population abundance because egg and larval mortality rates are positively correlated with initial egg production (Hewitt 1982), and hence adult abundance. Since 1980 anchovy abundance estimated (over the range of the stock by an ichthyoplankton survey) by the daily fecundity per gram of adult fish (estimated by histological examination of ovaries from adult fish, see Hunter and Goldberg 1980). The resulting egg production biomass estimates have been lower than simultaneous estimates of larva census biomass. The difference is due probably to an erroneous prior assumption concerning relative spawning frequencies of anchovies and sardines. Whereas the two species off California were assumed to spawn with equal frequency (Smith 1972), recent egg production method surveys in Peru indicate that the anchoveta *Engraulis ringens* spawns more frequently than does the sardine, *Sardinops sagax* (J. Alheit, PROCOPA, c/o IMARPE, Callao, Peru, personal communication).

By extrapolating egg and larva abundance-at-age back to the time of spawning, Lo (Southwest Fisheries Center, La Jolla, California, manuscript in preparation) has calculated an index of historic egg production. This index was analyzed by MacCall (1982) and Methot (1982) to produce a time series of estimated anchovy spawning biomasses from 1954 to 1982 (Figure 1). From very low abundance in the early 1950's, anchovy abundance increased, reaching an erratic equilibrium beginning about 1964. The increase in anchovy abundance lagged the sardine decline, and did not occur until sardine abundance dropped to one-tenth of its peak value. Whereas previous analyses indicated a peak anchovy abundance of four to five million mtons in 1964-66 (MacCall 1980), the new time series shows peak biomasses of about two million mtons to have occurred a decade later. Tentative biomass estimates for 1940-41 have been added to the time series, based on Smith's (1972) larva census estimates which are very similar to larva censuses for 1957-58 (Figure 1).

A reduction fishery was initiated in California in 1966, and a Mexican fishery expanded in the mid-1970's. Total annual harvests in 1980 and 1981 were about 300,000 mtons, very near the estimated MSY. Thus, the northern anchovy is "fully utilized" by common fishery standards. Recruitment has been highly variable since 1974, and has been declining since 1978. Unless recruitment improves, the anchovy resource is likely to continue to decline in abundance, given the current rate of exploitation.

Pacific Mackerel *Scomber japonicus*

Historical abundance of Pacific mackerel has been calculated by Parrish and MacCall (1978). Due to a string of very strong year classes, abundance in the 1930's probably exceeded average virgin stock levels (Figure 2; the fishery began about 1928). Over the following years spawning success (recruits per spawner) varied with a distinct six- to seven-year cycle which ended with collapse of the resource about 1965. A moratorium on Pacific mackerel catches was enacted by the State of California in 1970, and in 1972 the moratorium was supplemented by a formula for future harvests based on estimated stock abundance.

Subsequent recovery of the resource is documented by a series of annual reports to the California legislature (Richard Klingbeil, California Department of Fish and Game, Long Beach, California, unpublished reports). During the 1970's relatively strong recruitments occurred in even years (1972, 1974, 1976, 1978), showing a very different pattern of spawning successes than had occurred previously. The 1976 year class was sufficient to allow opening of a small fishery in 1977-78. The subsequent 1978 year class is probably the largest in the documented history of the fishery, and has supported increased harvests. The fishery and resource are now at historically high levels (Figure 2), and prospects are good that the fishery will continue indefinitely (at varying levels) under the present program of management.

Jack Mackerel *Trachurus symmetricus*

No substantial fishery has developed for jack mackerel in California or Mexico. A small fishery for young fish (less than age six) off southern California has existed since 1950, but the industry has had difficulty marketing the product. Much of the biomass consists of large adults in oceanic waters ranging from sourthern Baja California to the Aleutian Islands, and as much as 1500 km offshore. These fish may exceed 30 years of age (Fitch 1956), and stock size may be around two million mtons (MacCall and Stauffer 1983 in press).

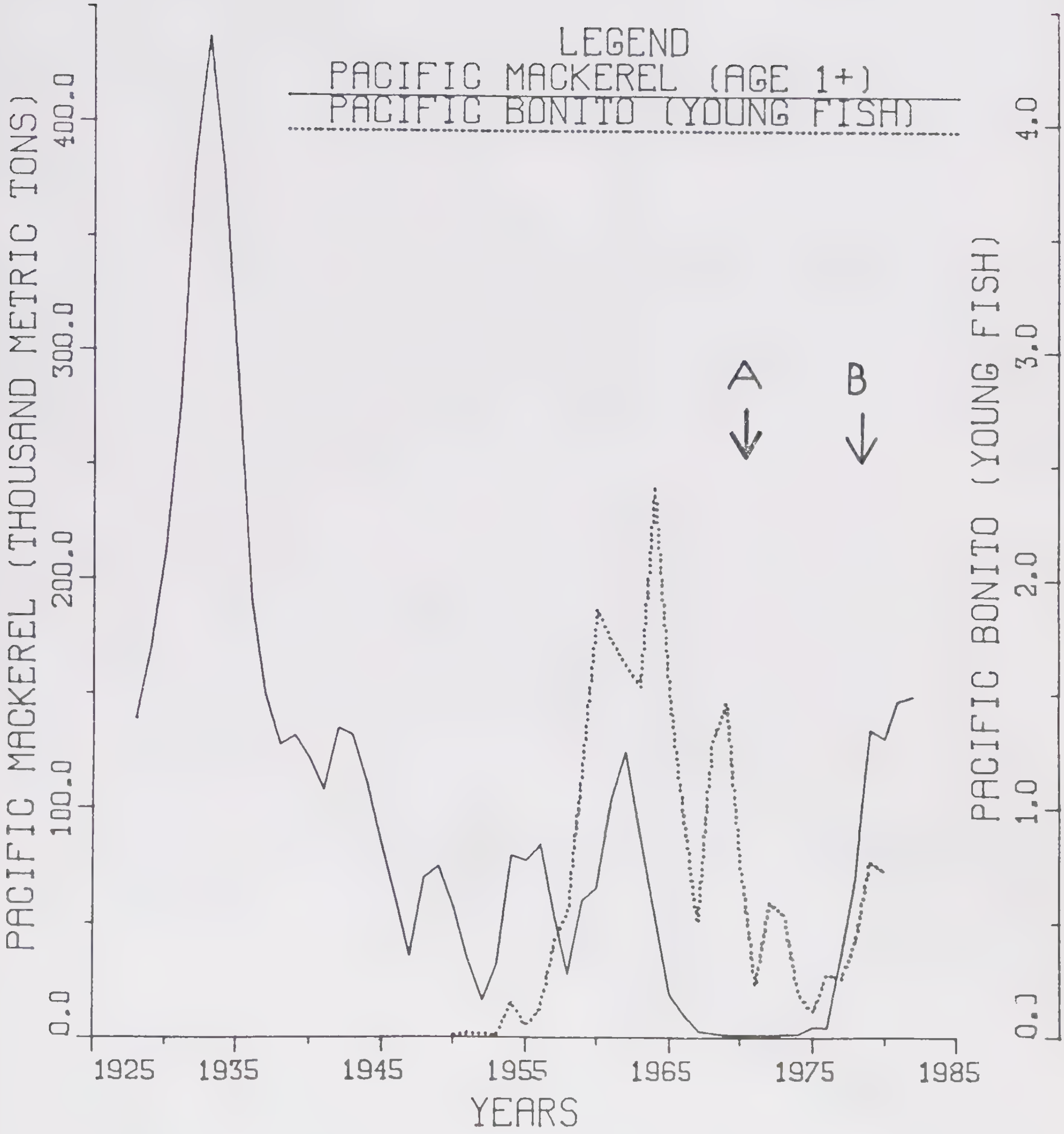

Figure 2. Time series of Pacific mackerel total biomass (age 1+) and Pacific bonito catch-per-effort. "A" denotes beginning Pacific mackerel fishing moratorium, and "B" denotes re-opening of the fishery.

Nearly all the spawning occurs in oceanic waters far from shore; however, subsequent young-of-the-year appear inshore, mainly off southern California. Recruitment strength is highly variable (Figure 3). Virtual recruitment strength was calculated by summing the percentage contributions of each year class to the fishery over the duration of the cohort. Strong year classes tend to be isolated by several weak year classes, with a suggestion of periodicity. Age compositions for more recent catches are unavailable, but the 1976 and 1982 year classes seem to be relatively prominent.

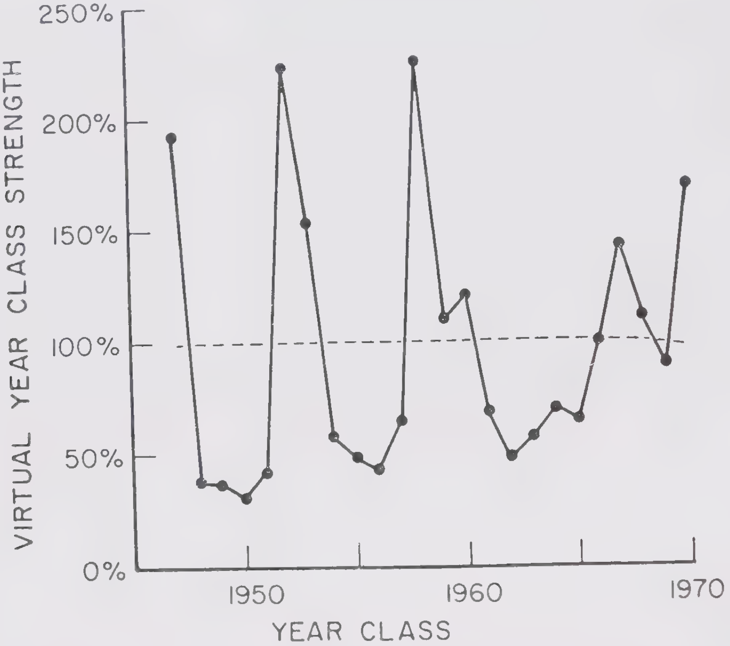

Figure 3. Virtual year class strengths of jack mackerel off California (from MacCall and Stauffer 1983).

LARGER COASTAL PREDATORY FISHES

Information on many of these fishes tends to be limited to catch histories and scattered biological observations with little continuity. Many of these fishes are migratory, with the bulk of the populations residing in Mexican waters. Migration strength is strongly associated with large scale ocean temperature anomalies (Radovich 1961), and the resulting environmental noise may conceal trends in stock abundance. These species are popular targets of both recreational fisheries and commercial fisheries, with catches of roughly equal magnitude.

Pacific Bonito *Sarda chiliensis*

Pacific bonito have long been visitors to California waters, with large adults appearing off southern California in the late summer and fall. However, an apparently self-sustaining younger population seems to have established residence in southern California waters only since the mid-1950's (see Collins et al. 1980 for a complete review). Recreational anglers catch mostly young fish, and catch-per-angler-trip is the best available index of the non-migrant stock (Figure 2).

Abundance has declined since the early 1960's. Some of that decline must be attributed to the commercial fishery which began harvesting bonito in 1966, but sustainability cannot necessarily be expected from a resource which has only recently come into existence. The bonito stock off California is a marginal population which hovers near the edge of viability--one hypothesis is that warm-water discharges from power generating stations have provided overwintering refuges for fish that would normally migrate south (Robson Collins, California Department of Fish and Game, Long Beach, California, personal communication). Faced with increasingly intense exploitation of pre-spawning fish, a minimum size regulation was implemented in 1982 in order to protect fish through their first spawning season. This management measure should help to maintain a southern California bonito stock during those periods when conditions are favorable.

California Barracuda *Sphyraena argentea*

Catch rates and size composition declined severely in the 1960s, leading to imposition of a strict size limit in 1972. This regulation caused a severe drop in U.S. recreational landings, but size composition has improved steadily over the past decade. Numerical abundance has shown little increase, but the improved spawning capacitiy of the stock has improved the prospects for recovery (Schultze 1983).

White Seabass *Atractoscion nobilis*

Recreational catch per effort has declined severely over the last 25 years, but commercial catch rates have remained relatively constant. Once abundant as far north as San Francisco, the range has steadily contracted southwards under exploitation (Collins 1982, Vojkovich and Reed 1983), indicating that population size may have declined more than local density would suggest. Mortality rate estimates calculated for the period 1958-60 (Thomas 1968) indicate that the fishing mortality rate (F) considerably exceeded the natural mortality rate (M). Perhaps due to the strong immigration of white seabass during the anomalously warm period of Thomas' study, he advocated increased fishing intensity. However, in light of more recent "rules-of- thumb" (e.g. Alverson and Pereyra 1969, Gulland 1970), which suggest that F is near M at MSY, the above relationship gives reason to suspect overfishing.

CAUSES OF FLUCTUATIONS

Fluctuations in fish stocks are caused by complex interactions of fishery, biological, and environmental factors. The social and economic tragedy that accompanies fishery collapses calls for "explanations," whereby people are eager to lay blame on the environment, the fishermen, or the government. There has been an unfortunate tendency toward simplistic single-factor explanations, and available data often are insufficient to explore more complicated hypotheses. In addition, scientists may interpret and "filter" data in favor of rationalizations and preconceived assumptions (Gould 1978). I suspect that analyses of stock fluctuations are especially prone to this problem. With hindsight, we can usually prescribe a management policy which would have averted the tragedy; such wisdom is much more difficult to apply with foresight. However, now with the cumulative experience of scores of similar fisheries and resources around the world, observed over decades of variability, fishery management is emerging from unexplored territory into a realm where experience provides a reliable guide. There will always be risk associated with these fluctuations; some of that risk can be reduced by appropriate resource management, and the remainder must be recognized as an unavoidable characteristic of the resource.

The fisheries and oceanography of the California Current are among the most thoroughly studied in the world. The California Cooperative Oceanic Fisheries Investigations (CalCOFI) Program, established over thirty years ago as a response to the collapsing sardine fishery, has provided a remarkable fishery-independent data base of physical and biological observations. This local knowledge is supplemented by experience in several analogous eastern boundary currents including those of Peru and South Africa (e.g. Bakun and Parrish 1980, 1982). This accumulation provides evidence for several mechanisms causing variability in coastal pelagic fish stocks, some of which will be reviewed briefly here (also see Lasker and MacCall 1983 in press).

Variability of Recruitment

Causes of recruitment variability is a popular area of fishery research, especially for coastal pelagic fishes (see Lasker 1981, and Sharp 1980 for reviews). As a source of stock fluctuations, recruitment variability is important in three cases: short-lived fishes, age class-specific fisheries, and high serial correlation of reproductive success. Population size behaves as an exponential moving average of recruitment strengths; variability of population size is therefore a function of the variability of recruitment itself and of the exponential decay coefficient or mortality rate. Fishes may be short-lived due to high natural mortality rates (e.g. anchovies) or due to high total (natural plus fishing) mortality rates (e.g. sardines). In the latter case, reduction of fishing intensity may help stabilize population fluctuations by averaging recruitment over longer periods. Age class-specific fisheries occur often as nursery ground fisheries such as the southern California jack mackerel fishery. Empirical probability distributions of reproductive variability can be developed in both of these cases. However the third case of high serial correlation is more insidious. The long-term probability distribution may be an inadequate description of near-term behavior, as near-term probabilities are conditional on current environmental or stock status. During long periods of good recruitment, the fishery may become overcapitalized. This tends to delay appropriate reductions in fishing intensity during the inevitable succeeding period of poor recruitment.

Climatic Change and Species Replacement

There is some dispute as to whether climatic regimes are distinguishable from the patterns of variability arising simply from an autoregressive mechanism. As in any correlation study, empiricalserial correlation spectra cannot be used to infer mechanisms, and existing time series of physical observations tend to be too short to test more sophisticated hypotheses. Recently Shuntov and Vasil'kov (1982) have suggested that sardine and anchovy variability may be driven by solar periodicity. Whichever the physical cause, biological systems tend to respond with regimes--protracted periods of similar behavior with abrupt transitions to a different mode of behavior.

The supposed "competitive replacement" of the sardine by the anchovy in California has now become a textbook case; the simulation study by Silliman (1969) was cited in Odum's (1971) ecology text as substantiation of the Volterra competition equations (Radovich 1981). This conclusion is very attractive to theoretical ecologists, whose mathematical models often have found little support in the real world. However, closer inspection (Daan 1980), and the following geographic argument severely weaken the case for simple competitive replacement.

The most important argument against competitive replacement is that the anchovy and sardine stocks have not occupied the same habitats. Typically, sardine stocks are distributed polewards of the respective anchovy stocks: The California sardine was abundant from Baja California to British Columbia, with a large portion of the population north of Pt. Conception, whereas the northern anchovy resides mostly south of Pt. Conception. Similarly, the Peruvian sardine is now abundant in northern Chile, whereas the previous anchoveta stock was scarce south of Pisco. There is evidence that the anchoveta resource has recently shifted southwards as well (Figure 4). A similar poleward shift in Peruvian fish production, although of unknown species composition, has been suspected for early historic times (Hutchinson 1950: p48), "It is also noteworthy that the rather unproductive region south of Pisco Bay, as far south as Iquique, seems from the 16th to the early 19th centuries to have been regarded as a more important source of guano than the central Peruvian coast...the only reasonable, though admittedly speculative, explanation of the decline of importance of the southern islands...is that minor changes in the dominant hydrographic pattern have occurred, tending to alter the distribution of the centers of abundant fish". Under the competitive replacement hypothesis, the replacing species should occupy the habitat of the former competitor. This does not seem to be the case for anchovies and sardines. Rather, geographic shifts of stock distribution indicate large scale environmental influences.

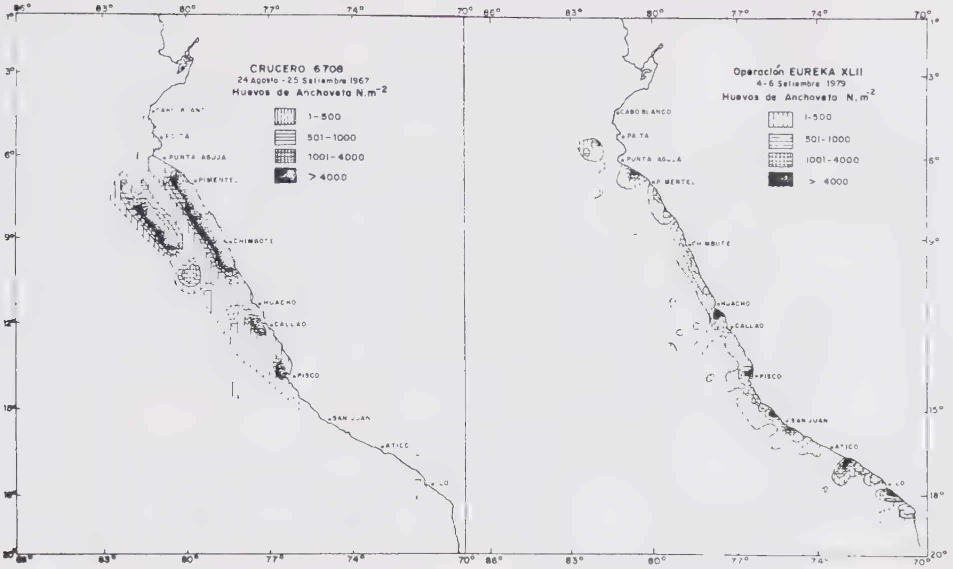

Figure 4. Sampling area and geographic distribution of anchoveta egg samples before and after 1971 (from Santander et al, 1982).

Variability of Natural Mortality Rates

Fishery models invariably assume a constant rate of natural mortality. Whether or not this is valid, fishery modelers have taken comfort in a long tradition of making this assumption. The quantity of fishery-independent information on California's anchovy stock has allowed Methot (1982) to attempt to reconcile age compositions with independent estimates of stock abundance. He concluded that the high anchovy biomass in the mid-1970s was not simply the product of strong recruitment, but rather was due to a substantial decrease in the natural mortality rate. If variability in natural mortality rate is a major factor in variability of pelagic fish stocks, methods such as cohort analysis are unreliable, and fishery-independent estimates of abundance are necessary. On the other hand, patterns of known variation in M may lead to development of meaningful multispecies fishery management models.

CONCLUSIONS

California coastal pelagic fish stocks show a variety of patterns of fluctuations. Pacific sardines have been depleted by excessive fishing pressure, and have been slow to recover. With some delay following the decline of the sardine, anchovies increased, reaching apparent equilibrium abundance in the mid-1960's. Both California and Mexico have developed reduction fisheries on anchovy, and the stock is now fully exploited. Pacific mackerel were depleted by the mid-1960's, but now have been rehabilitated due to favourable recruitment and strictly controlled harvest, and support a healthy fishery. Jack mackerel is a large resource, unfished except for a small fishery on the nursery grounds off southern California. Pacific bonito is a marginal population having recently established itself in southern California waters, and sustainability is questionable. The California barracuda resource is depressed, but age composition is responding favourably to a minimum size limit. The status of white seabass is somewhat unclear, but the resource is probably overexploited.

Variability in fish stocks can arise from many causes. Recruitment fluctuations are particularly important for short-lived fish. Species replacement seems to occur, but is environmentally mediated. Contrary to standard assumptions, changes in the rate of natural mortality of adults may be an important cause of fluctuations in abundance.

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POWER PLANT IMPACT ASSESSMENT: A SIMPLE FISHERY PRODUCTION MODEL APPROACH

ALEC D. MACCALL,[1] KEITH R. PARKER,[2] RONALD LEITHISER,[3] AND BILL JESSEE[3]

ABSTRACT

The relative abundance of a cohort affected by power plant entrainment mortality as a fraction (R_c) of the abundance of that cohort in the absence of power plant impact can be calculated by $R_c = \exp(-E_i t_i)$ where t_i is the duration of life stage i, and E_i is the entrainment mortality rate at stage i. Rate E_i can be estimated by the ratio of nonsurviving entrained organisms during a given time interval to the mean standing crop of stage i organisms in the source water during that interval. An estimate of adult abundance allows calculation of equivalent adult losses. When insufficient information is available to determine the long-term effect on the population, the fishery "potential yield" formula provides an interim estimate. Relative equilibrium abundance of the affected population (R_e) is approximated by $R_e = 1 - (\Sigma E_i t_i + F_p + F_f)/2M$, where F_p is adult mortality rate due to power plant impingement, F_f is adult mortality rate due to fisheries, and M is adult natural mortality rate. As in the case of the "potential yield" formula, this approximation of long-term equilibrium impact should be discarded when better estimates can be developed.

In recent years considerable effort has been expended in evaluating the impact of fish removals by intake cooling water systems at power plants in the United States. Methods of impact assessment are as diverse as the power plant sites at which the studies have been conducted, but may generally be classified into those which, according to Hackney et al. (1980), 1) offer an "expert" opinion as to the presence or absence of impact, or 2) are fish population models in which the sensitivity of the source water fish populations are examined under varying impingement rates.

The first category of assessments generally attempts to compare losses of organisms owing to power plant operation with sport and commercial fishery harvests and/or estimates of standing stock (DeMartini 1979). For adults, which are subject to impingement, comparison is fairly straightforward. However, for eggs and larvae, which are subject to entrainment, meaningful comparison is less direct. Goodyear (1978) extended a method proposed by Horst (1975) for treating entrained larvae in terms of equivalent adult losses which may then be considered alongside losses because of impingement. The second category of assessments includes more complex models using Leslie matrices (Vaughan and Saila 1976; Horst 1977; Vaughan 1981), differential equations (Hackney et al. 1980), or stock-progeny-recruit models (Christensen et al. 1977).

Several problems are inherent in many of these methods. There is an absence of an impact "scale" which enables the investigator to judge objectively the significance or insignificance of fish removals relative to the source water stock and to removals by fisheries. Additionally, sophisticated methods such as Leslie matrices and Goodyear's (1978) calculation of equivalent adult losses require life history parameters (i.e., fecundity, survivorship), which are often unknown for the species in question, and require substantial expenditures of time and money to obtain. Finally, these models may be difficult to interpret. While the investigator may understand the subtleties of interpretation, agency reviewers often lack the technical background to evaluate the results of complicated models.

The approach presented in this paper will alleviate many of the above problems. The proposed methods draw on techniques and models used in fishery management in order to provide a criterion for significance of impact. Indeed, the objectives of fishery stock assessment are very similar to those of power plant impact assessment. In both cases, we wish to know the effect of removals relative to what the stock can sustain through its density-dependent or other compensatory mechanisms. The models we propose do not require detailed life history information, and are sufficiently simple that the assumptions are apparent and results can be interpreted accordingly.

The methods may be separated into two somewhat independent analyses. The first is short-term assessment, which estimates entrainment impact on a

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[1] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[2] KRP Inc., 1837 Puterbaugh, San Diego, CA 92103.

[3] Lockheed Ocean Sciences Laboratory, 3929 Calle Fortunada, San Diego, CA 92123.

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single cohort (e.g., year class) in the sense of Goodyear's (1978) equivalent adult mortality. The second analysis estimates the long-term equilibrium impact of combined removals, including entrainment and impingement by one or more power plants, and all other nonnatural removals, including fishery harvests.

SHORT-TERM IMPACT

In the natural state, where no spawning products are removed by entrainment, the adult abundance of a cohort, N'_c (at a reference age T), is given by

$$N'_c = Pe^{-\int_0^T \mu(x)dx} \qquad (1)$$

where P is initial production of newly spawned eggs, x is age, and $\mu(x)$ is per capita natural mortality rate at age x, i.e., $-dN(x)/Ndx$.

A more convenient approximation of Equation (1) is

$$N'_c = Pe^{-\Sigma M_i t_i} \text{ and } T = \Sigma t_i \qquad (2)$$

where t_i is the length of age interval i, and M_i is a per capita natural mortality rate, assumed to be constant over interval i.

In the presence of mortality due to entrainment, the adult abundance of the impacted cohort, N_c (again at reference age T) is given by

$$N_c = Pe^{-\Sigma(E_i+M_i)t_i} \qquad (3)$$

where E_i is the per capita rate of entrainment mortality during age interval i.

The abundance of an impacted cohort relative to an unimpacted cohort is denoted R_c, and is given by

$$R_c = N_c/N'_c \qquad (4)$$

and after substituting Equations (2) and (3), this simplifies to

$$R_c = e^{-\Sigma E_i t_i} \qquad (5)$$

which is related to the conditional mortality rate (m) described by Ricker (1975: equation 1.9; here $m = 1 - R_c$). Note that T need not be specified, since we now need sum over only those age intervals in which E_i is nonzero. This is convenient since fish often cease being entrained at about the same time they cease being available to plankton sampling gear. More important is the fact that Equation (5) requires no knowledge of life history parameters. The main assumption here is that there is no compensatory change in the per capita rate of natural mortality during early life stages which offsets the added effect of entrainment mortality.

Equation (5) is similar in concept and derivation to recently published methods of calculating impact rate (e.g., Boreman et al. 1981; Jensen and Hamilton 1982). Those methods explicitly include water volumes and are especially appropriate to cases of highly fluctuating water flows. For the purposes of the assessment methods discussed in this paper, either method of calculating impact rate is applicable.

The entrainment mortality rates, E_i, are fairly easy to estimate. Larval mortality may be assumed to conform to a "Type 2 fishery" in the sense of Ricker (1975), wherein natural mortality occurs along with entrainment, and each occurs at a constant per capita rate during each age interval i. If power plant activity is fairly constant over the spawning season, each E_i is constant, and it is unnecessary to distinguish between Ricker's two types of recruitment. According to Ricker's (1975) equation 1.17, the quantity of larvae at stage i removed during a unit time by entrainment (L_i) is related to the mean abundance of larvae at stage i in the source water ($\bar{L}_i^*$) by the equation

$$L_i = E_i \bar{L}_i^* \qquad (6)$$

Therefore, E_i may be estimated by the equation

$$E_i = L_i/\bar{L}_i^* \qquad (7)$$

where L_i is a direct in-plant sample estimate of the quantity of stage i larvae entrained per day (or other convenient short time interval), and $\bar{L}_i^*$ is an estimate of the mean standing crop of stage i larvae over that same time interval in the source water, which may be estimated by quantitative plankton net tows. Note that entrainment rate E_i has units of inverse time according to the time interval used. Care must be taken to assure that time units are consistent throughout the analysis. Also note that i now refers to a stage, as it is generally most convenient to sort samples or planktonic larvae by size or stage categories. The length of time spent in each size category must also be determined. The most direct method may be to examine larval otoliths for daily growth rings (see Brothers et al. 1976) in order to ascertain the number of days (or other time unit employed) spent in stage i. Lacking this direct information on t_i, it may be necessary to assume that the larvae grow at the same rate as does some better known similar species in a similar environment.

Equivalent adult loss from a cohort (A_c) may be defined as

$$A_c = N'_c - N_c. \qquad (8)$$

However, a standing stock of adults often consists of several cohorts. Under the common fishery assumption that the age composition of the standing stock is at equilibrium, overall equivalent adult losses (A_e) from the stock are given by

$$A_e = N' - N \qquad (9)$$

where N' denotes unimpacted stock abundance, and N denotes impacted stock abundance, given the same initial production of eggs. Although this equilibrium assumption is often violated, it is nonetheless the basis of management of many fish stocks. Since the quantity R_c describes the ratio for a cohort N_c/N'_c, under equilibrium it also describes the population ratio N/N', here denoted R. The latter may be substituted into Equation (9) to give

$$A_e = N' \ (1 - R) \qquad (10)$$

or

$$A_e = N \ (\frac{1}{R} - 1). \qquad (11)$$

Thus equivalent adult losses can be calculated if adult abundance has been estimated, and this does not require the extensive knowledge of life history parameters demanded by Goodyear's (1978) approach.

Equations (10) and (11) raise a dilemma with respect to short- and long-term impact. Estimation of short-term impact has been based on the assumption of a fixed initial production of eggs. However, when real data are used, preimpact abundance (N') will usually arise from a larger egg production than does postimpact abundance (N), for the very reason than N' is larger than N, and egg production is itself dependent upon adult abundance. For this reason, Equation (10) is misleading, and will tend to overestimate the amount of adult equivalent losses actually occurring from an impacted stock at equilibrium. However, in most cases, preimpact abundance is unknown, and sampling programs produce estimates of N, which require application of Equation (11). Moreover, Goodyear's (1978) equivalent adult losses are calculated for an impacted stock making Equation (11) appropriate. As will be seen below, our method of estimating long-term equilibrium impact does not require explicit calculation of equivalent adult losses, and avoids the above complications.

LONG-TERM IMPACT

Whereas short-term impact may be described in simple terms of adult equivalent losses, long-term impact is more difficult to quantify. Short-term loss of adults implies loss of reproductive potential (egg production), and this loss is compounded over several generations. If compensatory mechanisms were not present, the impacted population would decline exponentially to extinction, given that it was in equilibrium prior to the impact. Fortunately, there are many types of compensatory mechanisms that allow the population to augment its reproductive rate so that it reaches a new equilibrium in the presence of an increased mortality rate (see Goodyear 1980). For example, lowered adult abundance may lead to increased per capita fecundity, decreased age of first reproduction, and/or increased survivorship at various life stages. Unfortunately, the actual mechanisms are poorly known and can be seldom quantified even for well-studied species. Detailed knowledge cannot be expected in routine impact analyses. Rather, we need simple approximations that will require a minimum of data.

Fishery management has long been concerned with the effect of removal (harvests) rates on fish abundance. Most of the work has been concerned with long-term equilibrium, and many fishery models are directly applicable to impact analysis. In particular, the "production model" (see Ricker 1975, Chapter 13), by means of simplifying assumptions, requires minimal knowledge of life history parameters. One of the simplest production models is the Graham-Schaefer model, which is constructed on the assumption of logistic population growth. The model assumes that equilibrium stock abundance declines linearly with an increasing rate of harvest (fraction of stock removed per unit time). The maximum net productivity in terms of total harvest by a fishery is therefore assumed to be achieved at a stock size which is exactly one-half the virgin level of abundance or carrying capacity, K (Fig. 1).

Normally, the production model is useful when a long time series of catches and fishing efforts (rates of removal) is available. In such cases, the production curve can be estimated from the data by statistical regression. On the other hand, there are many fisheries for which there is no history of exploitation, or for which the required data were never collected. Here, we may draw on the "potential yield" formula, first proposed by Alverson and Pereyra (1969), promulgated by Gulland (1970, 1971), and critically reviewed by Francis (1974). This approximation assumes that net productivity is maximal when abun-

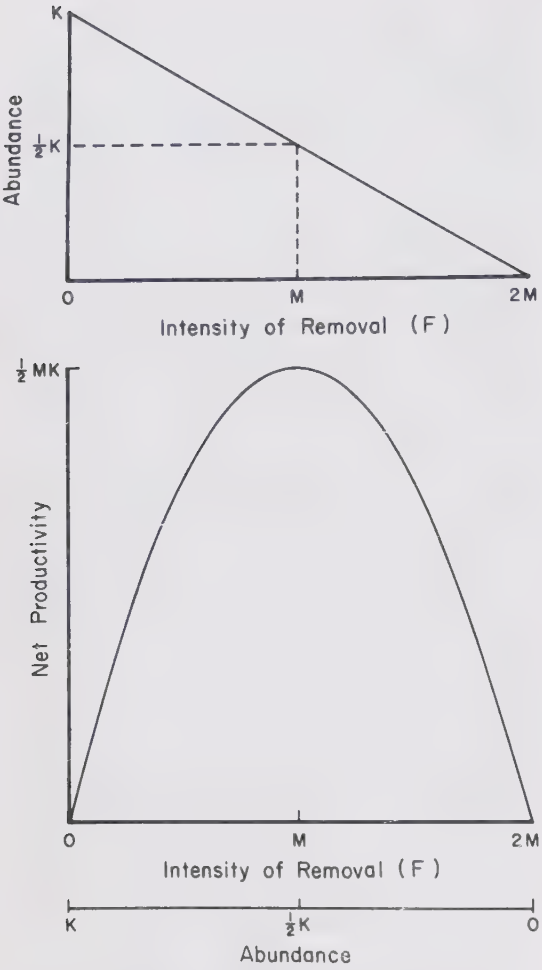

FIGURE 1.—The Graham-Schaefer production model scaled according to the "potential yield" formula (K is virgin abundance or carrying capacity, M is rate of natural mortality).

dance is at one-half the virgin level, and at this point the rate of fishery removals (F) is equal to the rate of natural mortality of adults (M). While many criticisms can be leveled at the potential yield formula, in actual practice it is often the only available basis of fishery management (e.g., North Pacific Fishery Management Council 1979a, b; Pacific Fishery Management Council 1982).

The production model corresponding to the potential yield formula is shown in Figure 1. The assumed relationship between equilibrium abundance (N_e) and rate of removal (F) is linear, giving the usual parabolic yield curve. Equilibrium abundance is at carrying capacity (K, denoted N'_e in this paper), when there are no removals. From inspection of Figure 1, the model predicts that equilibrium abundance falls to zero when the rate of removals is twice the rate of adult natural mortality (M). Thus, based on linearity, we have

$$N_e = N'_e \left(1 - \frac{F}{2M}\right) \qquad (12)$$

which predicts long-term equilibrium abundance in the presence of removal rate F. In parallel with our treatment of short-term impact, the long-term equilibrium abundance of a harvested or impacted stock relative to the abundance of the virgin stock is denoted R_e, and is given by

$$R_e = N_e/N'_e \qquad (13)$$

and according to Equation (12), we have the approximation

$$R_e = \left(1 - \frac{F}{2M}\right). \qquad (14)$$

Equation (14) says that we can estimate the impact of all removals, given the total rate of removals and the rate of adult natural mortality.

The total rate of removals (F) includes entrainment (E) and impingement (F_p) by all power plants operating in the area of the stock, and all fisheries (F_f) exploiting the stock:

$$F = \Sigma E + \Sigma E_p + \Sigma F_f. \qquad (15)$$

The removal rate due to entrainment (E) is estimated by the method presented in the previous section, i.e.,

$$E = \Sigma E_i t_i. \qquad (16)$$

Impingement (F_p) and fishing (F_f) mortality rates may be estimated by a method similar to Equation (7):

$$F_p = I/\bar{N}^* \qquad (17)$$

and

$$F_f = C/\bar{N}^* \qquad (18)$$

where I is the number of adults impinged in a year, C is the annual fishery harvest, and $\bar{N}^*$ is the mean abundance of the stock over the year.

The natural mortality rate is a difficult parameter to estimate. Ricker (1975) reviewed many of the methods. In some cases it may be necessary to assume a value of M, based on comparison with better known species. One useful method, based on comparative growth and environmental parameters, has been described by Pauly (1980). If a mortality rate can be estimated, for example, based on age frequency, the estimate will often be the total mortality rate of adults (Z), where

$$Z = M + \Sigma F_p + \Sigma F_f. \qquad (19)$$

The natural mortality rate can be obtained from

$$M = Z - \Sigma F_p - \Sigma F_f. \qquad (20)$$

If fish are being removed from the stock by several power plants and fisheries, the impact by a single entity cannot be considered in isolation. Our proposed method of long-term impact assessment allows an integrated assessment of impact, but also allows dissection into individual contributions to the total impact. Equation (15) states that the total rate of removals (F) is the sum of the individual instantaneous rates of removal. Since Equation (15) is a linear function, the fraction of the total impact which is attributable to any particular entity is the ratio of the sum of its contributions to total F from all sources as in Equation (15).

CRITERIA FOR IMPACT EVALUATION

Removal of fish from a stock, whether by a fishery or by a power plant, will usually lead to lowered equilibrium abundance. The previous section has presented a method for estimating the approximate reduction in abundance which has taken place. We must now determine whether this impact is "acceptable." In the case of a fishery where tangible values can be assigned to the catch and the stock, optimal catch rates and population sizes can be defined (Roedel 1975; Clark 1976). However, losses to a power plant produce no direct consumptive benefit, and, in many cases, the impacted stock is not subject to a fishery and therefore has no conventional value.

Fortunately, there exists a precedent for evaluating impacts on nonvalued species. The Marine Mammal Protection Act, enacted by the United States in 1972, requires that marine mammals be managed for optimum sustainable population size (OSP). Subsequently, the term was given a working definition: "Optimum sustainable population is a population size which falls within a range from the population level of a given species or stock which is the largest supportable within the ecosystem to the population level that results in maximum net productivity. Maximum net productivity is the greatest net annual increment in population numbers or biomass resulting from additions to the population due to reproduction and/or growth less losses due to natural mortality." (Gehringer 1976).

While power plants clearly do not directly impact marine mammals, the principle of optimum sustainable population size as defined above may be extended to fish and invertebrates as well. Since OSP is defined to fall within a range, impact is unacceptable when it causes population size to fall below the lower limit of that range, which is the point of maximum net productivity. In the logistic model assumed by our long-term impact assessment, maximum net productivity occurs at one-half the virgin, unimpacted population size. This gives a simple criterion for acceptable impact: Abundance should not be driven below one-half of its unimpacted level. In terms of the long-term impact model and its assumptions, this criterion is equivalent to saying that the rate of removal should not exceed the adult rate of natural mortality.

EXAMPLE APPLICATION

This example is based on data collected during 1978 for the purpose of estimating power plant impact on topsmelt, *Atherinops affinis*, inhabiting a California estuary.[4] Topsmelt is a bay-dwelling species with demersal eggs and a short (2-3 mo) spawning period. Topsmelt eggs hatch to produce 6 mm larvae, and larvae >15 mm are not entrained. Larvae were categorized by two length stages, 6-10 mm and 11-15 mm. Based on laboratory growth rate experiments for a closely related atherinid, the California grunion, *Leuresthes tenuis*, duration of these two stages is about 14 d each.

Standing stock and entrainment data (Table 1) are averages for the 3-mo spawning period based on biweekly sampling. Since larvae are concentrated near the surface during daylight hours, larval standing stock estimates are determined based on daytime surface larval densities sampled by a neuston net. These density values are extrapolated to the area of the estuary and a depth of 1 m. The mean entrainment rates are adjusted for variation in cooling water flow during each of the sampling periods. All entrained larvae are assumed to die. The short-term impact of the power plant is estimated to reduce recruitment strengths to 98% of their unimpacted value. Based on seine catches, the standing stock of adult topsmelt in the estuary was 5.4×10^5 fish. Since the power plant has long been operational, equi-

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[4] Because the power plant impact study has not completed the official review process, the proprietor wishes not to be identified at this preliminary stage.

TABLE 1.—Example calculation of short-term impact by entrainment of topsmelt larvae. n.e. indicates not estimated.

Stage	Entrainment (L_i) larvae/day	Standing stock (L_i^*) larvae	Entrainment rate (E_i) per day	Stage duration (t_i) days	$E_i t_i$
Eggs	0	n.e.	n.e.	n.e.	0
Larvae					
6-10 mm	4.0×10^4	5.3×10^7	7.5×10^{-4}	14	1.1×10^{-2}
11-15 mm	2.0×10^3	3.0×10^6	6.7×10^{-4}	14	0.9×10^{-2}
16 + mm	0	n.e.	n.e.	n.e.	0
Sum					2.0×10^{-2}

Equation (5): $R_c = \exp(-2.0 \times 10^{-2}) = 0.98$.
Equation (11): $A_e = 5.4 \times 10^5 (0.98^{-1} - 1) = 1.1 \times 10^4$ fish

valent adult losses are estimated by Equation (11) and are 1.1×10^4 fish.

Estimation of long-term impact requires information on all sources of mortality. The annual estimate of adult impingement by the power plant, based on 360 d of sampling, is 5,147 fish. According to California Department of Fish and Game records, there were no commercial landings of topsmelt in 1978, and recreational fishermen landed <1,000 topsmelt in this area (we use 1,000 fish for this example). Total mortality rate was estimated by regressing log abundance against age (Ricker 1975), giving an instantaneous total mortality rate (Z) of 1.8. Nonnatural mortality rates of adults were negligible (Table 2), giving a natural mortality rate of $M = 1.8$. Application of the long-term impact approximation (Equation (14)) indicates that topsmelt may be near 99% of their unimpacted abundance despite impacts by both power plants and fisheries. The majority of impact on the local resource is probably due to power plant operation, with entrainment impact being about twice as large as impingement impact. In any case, this estimated small reduction in long-term abundance indicates that there is no cause for concern with regard to power plant impact on topsmelt abundance in this estuary.

DISCUSSION

This approximation of long-term impact is not intended to be a substitute for proper studies of population dynamics. Rather, just as in the case of fishery management, it is intended to be a working approximation which should be discarded as more definitive information and analyses become available. In the case of impact assessment there will always be a suite of organisms, particularly invertebrates, which undoubtedly are impacted, but lack sufficient "status" to justify the expense of close monitoring and study. For these organisms, approximation is the most that reasonably can be asked. In this respect the potential yield approximation is well established in fishery management and should therefore be an equally applicable approximation for power plant impact assessment.

TABLE 2.—Example calculation of long-term impact from all sources of topsmelt mortality.

Source of impact	Catch (fish)	Mean standing stock (fish)	Coefficient of mortality
Impingement	5,147	5.4×10^5	1.0×10^{-2} (F_p)
Fishery	1,000	5.4×10^5	0.2×10^{-2} (F_f)
Entrainment	(see Table 1)		2.0×10^{-2} ($\Sigma E_i t_i$)
Sum			3.2×10^{-2}

Equation (20): $M = 1.8 - 1.0 \times 10^{-2} - 0.2 \times 10^{-2} = 1.8$
Equation (14): $R_e = 1 - (3.2 \times 10^{-2}/3.6) = 0.99$.

It is likely that the bases of the approximation can be improved in two ways. First, organisms may be classifiable into types with various productivity curves, of which the logistic is a special case. For example, Fowler (1981) observed that species with high reproductive rates and short life-spans show most density-dependent compensation at low population levels, whereas species with low reproductive rates and long life-spans show most of their density-dependent compensation near carrying capacity. Thus, it may be possible to specify the shape of the curves in Figure 1 as a function of observable or measurable traits of specific organisms. The second improvement consists of developing better scaling criteria for the production curve, once its shape has been established. A survey of population growth rates of many species could form the basis of an empirical estimator of compensatory capacity; the use of natural mortality rate may not be appropriate in many cases. Clearly, an improved approximation method would be of value both to fishery management and to power plant impact assessment.

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BIOLOGY AND FISHERY POTENTIAL OF JACK MACKEREL *(TRACHURUS SYMMETRICUS)*

ALEC D. MACCALL
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038

GARY D. STAUFFER
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Northwest and Alaska Fisheries Center
Seattle, Washington 98112

ABSTRACT

Young jack mackerel (age 0 to about 5 years) are most abundant in the Southern California Bight, where they school in open waters and near offshore banks. They progressively emigrate from these grounds, but the whereabouts of 6- to 15-year-old fish is not well known. The large fish, 15 to 30+ years old, school offshore in open ocean waters from Baja California to the Aleutian Islands. Ages 1 and older are capable of spawning, an exceptionally early age of maturity for a long-lived species. Spawning extends from central Baja California to British Columbia, with a tendency for larval abundance to progress northward from late winter to late summer. The Southern California Bight contains few jack mackerel larvae until late in the spawning season.

Year-class strengths are highly variable, with strong year classes typically separated by several relatively weak ones. On the basis of larvae collected on CalCOFI surveys, spawner abundance has been fairly constant since 1950. Spawning biomass is estimated to be 0.64 to 1.3 million metric tons (MT) in the CalCOFI region, with perhaps an equal biomass outside that region.

The estimated spawning biomass was allocated among age categories according to assumed mortality rate schedules. Because of age-specific mortality rates, potential yield was estimated by applying the Gulland approximation to each age category separately and summing the results. Overall potential yield estimates range from 130 to 260 thousand MT. The young inshore fish have a potential yield of 100 to 200 thousand MT, whereas the old offshore fish have a potential yield of 10 to 25 thousand MT. If a significant fishery were to develop on either segment, the other segment would probably be impacted indirectly.

RESUMEN

Jureles (*Trachurus symmetricus*) jóvenes, de hasta 5 años de edad son abundantes en el seno del sur de California, y sus cardúmenes se presentan en mar abierto y en las proximidades de los bancos costeros. Los jureles emigran progresivamente desde estas zonas, pero no se conoce con la debida precisión el paradero de las poblaciones con edades entre 6 y 15 años. Jureles grandes, de más de 30 años de edad integran los cardúmenes de mar abierto, desde Baja California hasta las Islas Aleutianas. Los jureles inician la reproducción al año de edad, madurez precoz y excepcional en peces que llegan a alcanzar una larga vida. La puesta se extiende desde Baja California hasta la Columbia Britanica, con una tendencia a que la abundancia de larvas progrese hacia el norte, desde finales del invierno hasta finales del verano. La zona del seno del sur de California contiene pocas larvas de jurel hasta el final de la época de puesta.

La dominancia de las generaciones es muy variable, observándose generaciones abundantes alternando con otras de escasez numérica. La abundancia de reproductores, tomando como base las larvas recolectadas durante las exploraciones del programa CalCOFI, resulta bastante constante desde 1950. La biomasa de reproductores en la región explorada por el programa CalCOFI se ha estimado entre 0.64 a 1.3 millones de Tm., y se considera que la cantidad será aproximadamente similar para las zonas adyacentes a esa región.

La biomasa estimada se distribuye entre categorías de edades de acuerdo con el valor asumido establecido para la mortalidad. Considerando los valores de mortalidad para las diversas edades se estimó el rendimiento potencial, aplicando la aproximación de Gulland separadamente para cada categoría de edad y sumando luego los resultados. Se estima que el total de rendimiento potencial oscila de 130 a 260 mil Toneladas. Los peces jóvenes costeros presentan un potencial de producción de 100 a 200 mil Toneladas, mientras que los oceánicos tendrían un potencial de rendimiento de 10 a 25 mil Toneladas. Si se desarrollase una pesquería importante en cualquiera de estos sectores, el otro sería afectado indirectamente por dicha pesca.

FISHERIES AND DISTRIBUTION

The jack mackerel, *Trachurus symmetricus*, was reported in the commercial landings of fish in California as early as 1888, but was of minor commercial importance before 1947. Of much greater commercial importance were the more profitable Pacific sardine,

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Sardinops sagax caerulea, and the more desirable Pacific mackerel, *Scomber japonicus*. Much of the jack mackerel catch between 1926 and 1946 was absorbed by fresh fish markets and consisted primarily of fish taken from mixed Pacific sardine and Pacific mackerel schools. Landings were low, varying between 180 and 14,000 MT. During these years, the fish were referred to as horse mackerel and had relatively little market appeal. In 1947 the fishing industry, after being hit hard by poor sardine landings, turned to jack mackerel and landed 58,535 MT. The following year, the U.S. Food and Drug Administration authorized the common name jack mackerel for use on labeling. This was expected to have greater consumer appeal than the original name horse mackerel. Jack mackerel have been a major contributor to California's commercial landings ever since (Figure 1).

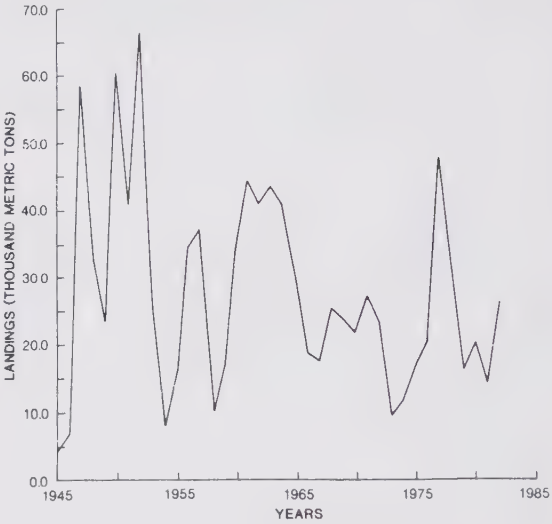

Figure 1. California jack mackerel landings (source: California Department of Fish and Game).

There is presently only one fishery targeting on jack mackerel. This fishery uses purse seine gear, and operates out of southern California ports, harvesting small fish from local waters. Fisheries farther to the north take jack mackerel incidentally. The salmon troll fisheries operate in nearshore waters north of Point Conception, and take an unknown but probably large number of jack mackerel, which are discarded at sea. The foreign trawl fleets, which operate offshore north of Point Arena, take jack mackerel incidentally to fishing for Pacific whiting (*Merluccius productus*), but have actually avoided taking jack mackerel in recent years. If an expanded domestic offshore trawl fishery develops out of northern California and Oregon ports, large jack mackerel may become a target species, and will almost certainly be an incidental species of significant magnitude. Recreational fisheries all along the Pacific coast occasionally take jack mackerel but do not consistently target on the species. The various jack mackerel fisheries are described in detail by MacCall et al. (1980).

In the Vancouver Island area of Canada, large jack mackerel have been caught at the surface by purse seiners and are taken incidentally in the bottom trawl fisheries (Hart 1973). Although jack mackerel are quite abundant at times, there is no directed fishery for the species. Incidental catches are insignificant and are not included in catch records (S.J. Westrheim, Pacific Biological Station, Nanaimo, B.C., pers. comm.).

The distribution of jack mackerel extends northward into the Gulf of Alaska east of 160° W. A high-seas experimental salmon gill net survey found jack mackerel to be relatively abundant (Larkins 1964). Incidental catches along the coast of southeast Alaska occur infrequently and are not documented (D. Cantillon, Alaska Department of Fish and Game, Juneau, Alaska, pers. comm.). Jack mackerel have been found as far south as Cape San Lucas, Baja California. The offshore limit of the population is poorly defined, but various sources have been compiled by Blunt (1969) to produce a distributional map (Figure 2). The offshore limit is approximated by a line running from Cape San Lucas, Baja California, to the eastern Aleutian Islands, Alaska. A large portion of the range lies outside the 200-mile fishery jurisdiction zones of the U.S. and Mexico.

REPRODUCTION AND STOCK STRUCTURE

In their study of maturation of jack mackerel from the southern California fishery, Wine and Knaggs (1975) determined that most females become sexually mature at about their first birthday. Although immature fish were found at all times of the year, 50% or more of all females appear to be close to or in spawning condition from March through September. Very young spawners appear to reach a reproductive condition later in the season than do older spawners. Nothing is known of the maturity cycle of the large offshore fish.

MacGregor (1976) calculated the fecundity, in advanced eggs per gram of fish, of thirty jack mackerel. These fish could be divided conveniently into two distinct groups, representing small and large fish. The small fish ($n = 15$, $\bar{l} = 235$ mm) had a mean fecundity of 68.5 advanced eggs per gram of fish. The large fish ($n = 15$, $\bar{l} = 519$ mm) had a mean fecundity of

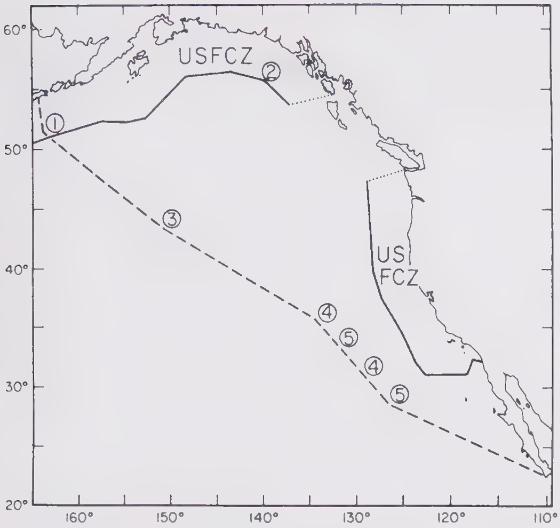

Figure 2. Distribution of the jack mackerel resource (modified from Blunt 1969). Circled numbers indicate the periphery as determined by various sampling methods: (1) gillnet catches, INPFC, 1963; (2) gillnet catches, INPFC, 1955; (3) eggs and larvae, NORPAC, 1955; (4) night-light stations, CDF&G, 1957-68; (5) eggs and larvae, CalCOFI, 1950-78.

152.3 advanced eggs per gram of fish. The small fish, which would correspond to age 2 years, had a fecundity of 65.8/152.3 = 0.43 relative to the large fish on a per unit body weight basis.

Jack mackerel eggs and larvae first become abundant in the waters far offshore of northern Baja California and southern California in March through June (Kramer and Smith 1970; Ahlstrom 1969). There is very little production of eggs and larvae in the Southern California Bight until July and August, presumably when the younger fish begin to spawn (see above). Also, the center of offshore spawning loosely moves north as the summer progresses. The northern and offshore areas of spawning have received very little sampling effort, so the seasonality and geographic limits to spawning by the offshore population are poorly known. A survey of the northeastern Pacific in August 1955 took jack mackerel eggs and larvae off Oregon and Washington from 100 to 1000 miles offshore (Ahlstrom 1956). CalCOFI cruise 7210 (October 1972) similarly found a large isolated area of spawning jack mackerel extending from 200 to 600 miles off the coast of Washington, verifying the existence of late northern offshore spawning. The northern limit of jack mackerel spawning was not determined.

There are two distinct and non-overlapping segments shown by available length frequencies (Figure 3). The southern California purse seine fishery presently catches fish ranging from 10 cm to 30 cm FL, whereas offshore and northern coastal captures tend to range from 50 cm to 60 cm FL. The intermediate lengths are distinctly lacking in either data set. The southern California fleet captured moderate quantities of fish ranging from 30 cm to 40 cm FL during the early years of the fishery (Figure 3), but whether this reflected biological availability, fishermen's tactics, or fishing pressure is not known. Length frequencies of jack mackerel taken off Monterey from 1958 to 1967 (not shown) resemble those of the early southern California fishery. The Monterey fish were slightly larger, with one-half of the catch ranging from 30 cm to 40 cm FL, but with few fish larger than 40 cm FL. Length frequency of jack mackerel captured by the California Department of Fish and Game's preseason offshore albacore cruises shows a few fish ranging from 40 cm to 50 cm FL, but no data show the 30-cm-to-50-cm fish in the abundance they must presumably have, assuming that the small fish eventually grow and join the large fish segment. Soviet research trawls taken from 1966 to 1977[1] show a clear geographic pattern of jack mackerel mean lengths, with small fish (20-30 cm FL) to the south and inshore, and large fish (ca. 53 cm FL) to the north and offshore.

As shown above, jack mackerel eggs and larvae are distributed widely in the northeastern Pacific. The quantity of spawning products released in the Southern California Bight is a small portion of the total. Nonetheless, the largest known concentrations of young-of-the-year jack mackerel are found in the Southern California Bight. Many of the southern California fish are undoubtedly spawned locally. However, it is likely that the extensive offshore spawning by large fish produces significant numbers of offspring and, judging from the scarcity of juvenile jack mackerel elsewhere, we believe these fish find their way to the Southern California Bight. Anecdotal evidence of this movement has been provided by the discovery of many young-of-the-year jack mackerel in albacore (*Thunnus alalunga*) stomachs taken off the coast of California in the summer of 1982 (M. Laurs, Southwest Fisheries Center, La Jolla, California, pers. comm.). Thus it is reasonable to assume that the southern California segment of the jack mackerel population is not self-sustaining, but depends to an unknown extent on spawning by the offshore large fish segment.

RECRUITMENT

Absolute magnitude of recruitment cannot presently be determined. However, examining the contributions

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[1] Stepanenko, M. A. Some traits of biology and reproduction rate and conditions of California jack mackerel. Presented to the 1979 U.S.-U.S.S.R. Bilateral Meeting on Fisheries Assessment in the North Pacific, Seattle, June 5-8, 1979.

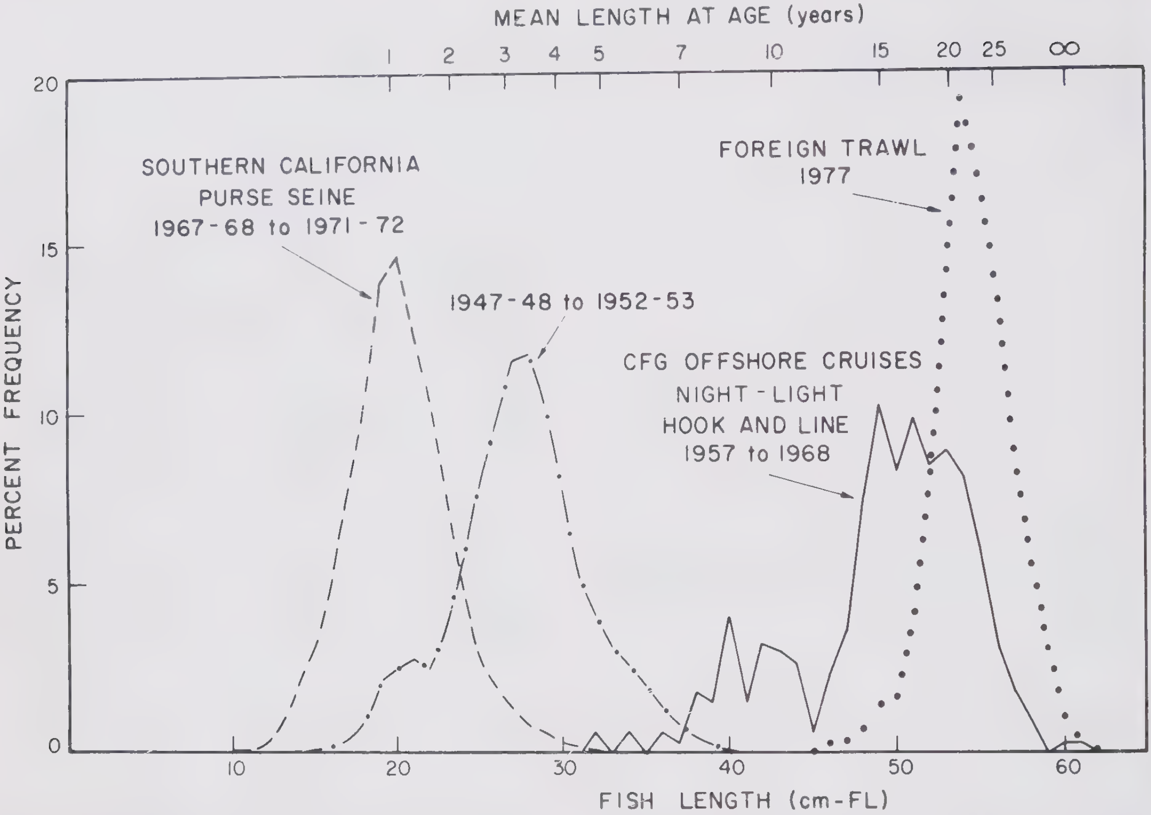

Figure 3. Length frequency of jack mackerel taken by various fishery segments and surveys. Age scale is not an accurate measure of age at length, and is provided only for comparison.

of various year classes to the southern California fishery provides a rough picture of recruitment variability. The fishery landings have been determined by processor orders rather than by availability, so actual volume of catch is not necessarily a good indicator of relative abundance. Virtual year-class strength, obtained by summing the percentage contributions of a year class to the various seasons in which it was fished, provides a rough indication of year-class variability. Age composition data were taken from Knaggs (1974a, b), Knaggs and Barnett (1975), Fleming and Knaggs (1977), and Fleming (California Dept. of Fish and Game, Sacramento, Calif., pers. comm.). Because we have used percentage contribution, an average year class will have a virtual strength of 100%. Long-term trends cannot be detected by this treatment, since year classes are effectively compared only with their near neighbors.

The resulting series of virtual year-class strengths (Figure 4) shows a pattern of runs of weak year classes interrupted by occasional strong year classes. Until the 1966 year class, recruitment seems to have been either very good or very poor, with average recruitment a rarity. In more recent years, since 1966, year classes seem to have fluctuated less severely; however, the recent fishery, from which data are not yet fully available, suggests that the 1976 year class was very strong. The 1982 year class also appears to be extraordinarily abundant, based on high catch rates by a midwater trawl survey for young fish in the Southern California Bight (Mais 1982) and on the occurrence of young fish in albacore stomachs cited above.

ABUNDANCE

CalCOFI ichthyoplankton surveys are the principal source of information on jack mackerel spawner abundance. Because the CalCOFI region does not encompass the full range of the fish (see Figure 2), some assumptions are necessary. Principally, we assume that the density of fish in the CalCOFI region bears a reasonably constant relationship to the size of the total spawning population. CalCOFI surveys have shown

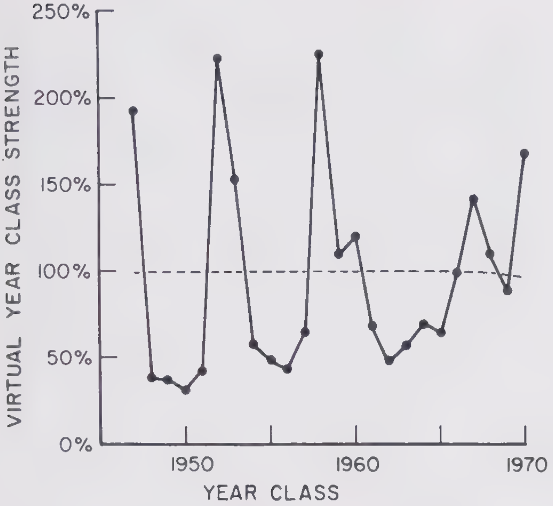

Figure 4. Relative recruitment strengths of jack mackerel year classes in southern California. Virtual year-class strength is measured by the sum of percentage contributions to seasonal landings over the lifetime of the year class. The dashed line indicates average strength.

that the center of spawning moves northward as the season progresses, from northern Baja California waters in March and April to as far north as Oregon in the fall (Ahlstrom 1956, 1969; Kramer and Smith 1970). Whether this shift is due to actual migration of spawners or to progressively later maturation of more northerly fish is not known.

Mean apparent density of jack mackerel larvae was calculated from CalCOFI samples in regions most consistently occupied by eggs and larvae. This density is the average quarterly density off northern Baja California in the first and second quarters of the year, and off southern California in the second and third quarters. The near inshore regions of Baja California and southern California were excluded. The densities are plotted in Figure 5. The unusually low densities from 1958 to 1961 may be due to the influence of abnormally warm oceanic temperatures from 1957 to 1960: the population may have shifted northward; gonadal maturation may have been affected; and abnormally rapid growth of larvae would decrease apparent abundance. Also, it is highly unlikely that abundance changes of the magnitude suggested by the larval density can actually occur, given the low rate of mortality exhibited by offshore jack mackerel. Data for 1958-61 will not be considered as representative of jack mackerel abundance during that period.

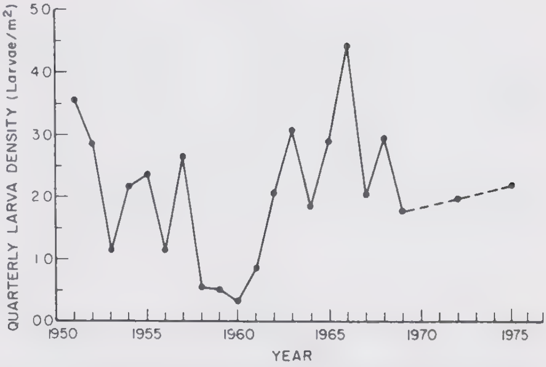

Figure 5. Density of jack mackerel larvae in selected areas of CalCOFI surveys.

Larval densities show considerable year-to-year fluctuation (Figure 5), but there is no trend showing a long-term change. It would be difficult to show small changes in future jack mackerel abundance using the CalCOFI larval density because of natural variability and anomalies like those of 1958-61. Thus a minimum management response time to a decrease in abundance is probably greater than 6 years, given the present triennial schedule of CalCOFI surveys.

Ahlstrom (1968) estimated the jack mackerel resource to be 1.9 to 4.4 million MT of spawning biomass. Ahlstrom based his estimate on CalCOFI survey estimates of jack mackerel egg production (Farris 1961). He used two assumptions of fecundity: the low fecundity estimate was two spawning batches per year, based on the two modes of egg diameters observed in ovaries by MacGregor (1966); the high fecundity estimate was 3⅓ batches per year, based on a peak egg abundance (when all fish are assumed to spawn) to average egg abundance, and assuming that it takes at least 30 days to mature a batch of eggs. Ahlstrom also assumed that the total stock was 1½ to 2 times that measured in the CalCOFI area.

Knaggs (1973) used tag returns to estimate the total population available to the wetfish fleet off southern California. This estimate was 0.6 to 1.4 million MT, but must be considered tentative because sample size was very small, and many assumptions underlying tagging estimates could not be met.

Pashchenko[2] used an acoustic-trawl survey to estimate the jack mackerel biomass *outside* the CalCOFI area in the spring of 1978. Using the assumption that all fish in the path of the net were caught, he obtained a biomass of 308,000 ± 91,000 MT. If a portion of the fish in the trawl path were escaping capture, his estimate should be increased accordingly.

Pashchenko, V. M. Distribution, biology and biomass assessment of the jack mackerel *Trachurus symmetricus* (Ayres). Presented to the 1979 U.S.-U.S.S.R. Bilateral Meeting on Fisheries Assessment in the North Pacific, Seattle, June 5-8, 1979.

We propose a new estimate of jack mackerel abundance. The approach is similar to Ahlstrom's, but assumptions regarding fecundity can be improved in light of recent work on other species (see below). Also, the methodology is changed slightly, and additional factors are considered in estimating egg production rates.

Egg production can be expressed by the following equation (Parker 1980):

$$E = Brfp \tag{1}$$

where E is daily egg production, B is spawning biomass, r is fraction of the spawning population that is female, f is fecundity in eggs per body weight per spawning, and p is fraction of females spawning per day.

The equation can be rearranged to

$$B = E/rfp \tag{2}$$

in order to estimate spawning biomass.

Egg production in the CalCOFI region for the years 1951-54 was estimated by Farris (1961). As was shown above, there is no visible trend in jack mackerel abundance since that time, so Farris' data are appropriate for estimating present biomass. Farris corrected his egg production estimates for a 3-day duration to hatching; however, he ignored the effects of natural mortality. Because of losses of eggs before hatching, the duration of an average egg would be somewhat less than 3 days. Paul Smith (Southwest Fisheries Center, La Jolla, Calif., unpublished data) has calculated approximate numbers of jack mackerel eggs surviving to each stage of development at 15°C. Time to hatching at 15°C is 86.4 hours, whereas mean duration of eggs is 53.2 hours, eggs being terminated either by mortality or by hatching. Thus the mean duration is 0.62 of the time to hatching. Farris' eggs were in an environment averaging 15.5°C, which is reasonably close to the above temperature. This change in assumed residence time requires that Farris's egg production estimate be multiplied by 1/0.62, or 1.62.

Peak egg production extends from March to June in the CalCOFI area, during which period 82.6% of the total year's eggs are released. Average egg production for March through June is 5.5×10^{14} eggs or 4.5×10^{12} eggs/day (Farris 1961). With the above mortality correction, the latter value is increased to 7.3×10^{12} eggs/day.

Ahlstom (1968) used a fecundity estimate of 306 eggs/gram/spawning, based on a single fish examined by MacGregor (1966). MacGregor (1976) gives fecundities of 30 fish, including 15 fish longer than 40 cm. The mean fecundity of these large fish was 153.2 advanced eggs/gram body weight, or about one-half the earlier estimate. Our biomass estimate will use MacGregor's fecundity estimates. However, it is likely that they are low. Pashchenko[3] examined 18 large female jack mackerel taken 390 miles west of San Diego in the spring of 1978. These fish were larger (mean 54.0 cm FL) than MacGregor's fish, and had a mean fecundity (362.6 eggs/gram) over twice that obtained by MacGregor. If Pashchenko's data are used, or are averaged with MacGregor's observations, resulting biomass estimates would be considerably lower.

Little is known of spawning rates of pelagic fish, and nothing is known for jack mackerel. Ahlstrom (1968) used a minimum estimate of two spawnings per year, because there were two modes of egg diameters in the single fish examined; and he used 3.3 spawnings per year as a high estimate, assuming 30 days is necessary to mature each batch of eggs. In comparison, similar spawning rates were suspected for the northern anchovy (*Engraulis mordax*), for essentially the same reason. However, recent work on anchovy gonad histology (Hunter and Goldberg 1980) has strongly indicated that about 15% of the mature female anchovy population is spawning each day during the peak spawning months. This spawning rate translates as approximately one spawning per week, and indicates that a batch of eggs may require fewer than 7 days to be produced. Because jack mackerel gonad morphology and the protracted spawning season are similar to those for anchovy, we assume that spawning rates are similar to those for anchovy. In our estimate of jack mackerel abundance we will use 15% spawning per day as an arbitrary upper limit, and 7.5% spawning per day as a lower limit. Lower percentages could be considered; the biomass estimate changes inversely with this percentage, which is a major source of imprecision. It is assumed that males exist in equal weight to females, so the proportion of females is 0.5.

Using the values in equation (2), $E = 7.3 \times 10^{12}$ eggs/day, $r = 0.5$, $f = 152.3$ eggs/gram of large female fish, $p1 = 15\%$ female fish spawning/day, $p2 = 7.5\%$ female fish spawning/day, we obtain spawning biomass estimates of 0.64 and 1.3 million MT in the CalCOFI region. If the fish migrate extensively, with virtually all fish spawning in the CalCOFI region and then dispersing, these may be direct abundance estimates. If the fish are less migratory, and only a fraction of the population spawns in the CalCOFI region, total abundance will be greater. Ahlstrom (1968) assumed that one-half of the total jack mackerel spawning biomass resides outside the CalCOFI area. Pashchenko[4] also feels that one-half of the resource may be spawning outside the CalCOFI area. Although the exact fraction of the resource outside the CalCOFI area cannot be quantified, we will assume the total spawning biomass to be 1.36 million MT (1.5 million short tons) as the working estimate.

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[3] See footnote 2

This working estimate of 1.36 million MT of spawning biomass is considerably lower than Ahlstrom's (1968) range of 1.9 to 4.4 million MT. However, it is more consistent with current knowledge of the likely spawning frequency of pelagic fishes. This working estimate would suggest that available southern California biomasses are smaller than estimated by Knaggs (1973). However, Knaggs's estimate may be high because of emigration, and our estimate gives total biomasses approaching Knaggs's lower range of 0.6 million MT.

MORTALITY RATE

The natural mortality rate of jack mackerel has not been estimated previously. The necessary data for a direct estimate are very difficult to obtain, given the stock structure and poorly known migratory habits of the fish. Because of the size selectivity and geographic character of existing fisheries, age-frequency analysis is not feasible because mortality rates are confounded with rates of emigration. However, other information correlating with mortality rates is available, allowing reasonable values to be hypothesized. Pauly (1980) examined a large number of fish stocks, from which he derived an empirical natural mortality rate approximation based on von Bertalanffy growth parameters and water temperature. Wine and Knaggs (1975) obtained von Bertalanffy parameter estimates of the asymptotic length ($L_\infty = 60.3$ cm) and the growth rate coefficient ($K = 0.0935$/year). Using the 10-m annual mean water temperature off central California of about 14°C (Lynn 1967), Pauly's method gives a tentative natural mortality rate of $M = 0.23$. Fitch (1956) reports that some large jack mackerel are over 30 years of age, according to growth rings on their otoliths. The average mortality rate would have to be quite low to allow a significant number of fish to reach such an age, confirming the magnitude of the Pauly approximation.

It is highly unlikely that jack mackerel exhibit a constant natural mortality rate throughout their life. Small young fish living in the predator-rich nearshore area are likely to have much higher mortality rates than the large offshore fish. Based on this speculation, the following age-specific natural mortality rate schedule is postulated for jack mackerel: $M_0 = 0.5$, $M_1 = 0.5$, $M_2 = 0.45$, $M_3 = 0.4$, $M_4 = 0.35$, $M_5 = 0.3$, $M_6 = 0.25$, $M_{7+} = 0.2$. Other tentative mortality rate schedules could be proposed (see MacCall et al. 1980).

FISHERY ANALYSIS AND POTENTIAL YIELD

A simple "piece-wise" dynamic pool model can be used to represent the long-term average or steady-state population structure. Natural and fishing mortality rates and weights at age are used to estimate relative biomass at age from the working estimate of 1.36×10^6 MT (1.5×10^6 short tons) spawning biomass. The total spawning biomass is allocated among the ages according to these relative contributions. The biomass of young of the year (age 0.5) was calculated by the ratio of cohort weights at age 0.5 and age 1.

As discussed previously, it is likely that young jack mackerel have a lower batch fecundity and may spawn fewer times than do older mature fish. Spawning biomass, being based on egg censuses, is expressed in terms of body weight equivalents of fully mature spawning females. Total fishable biomass is therefore likely to be greater than spawning biomass. Two alternative fecundity models are used here. The first model simply assumes that all fish are equally fecund on a unit body weight basis (Table 1). The second model assigns partial fecundities to young fish. If mature fecundity is given a relative value of 1.0, ages 1 through 4 are assigned relative fecundities of 0.2, 0.4, 0.6, and 0.8, respectively (Table 2).

The above method of allocating biomass among age categories is subject to considerable imprecision. Both assumed rates of natural mortality and relative fecundity of young fish have strong influences on the age structure and total biomass of the model population. Since the spawning biomass is fixed, different mortality rate schedules will result in inverse changes in allocation of biomass to small fish (ages 0-8) and large fish (ages 15-30). As can be seen in Table 2, assumption of reduced fecundity of young fish results in an increase in estimated total biomass.

The dynamic pool model was used to estimate fishing mortality rates by an iterative process. Fishing mortality rates at age (F_j) are given by

$$F_j = C_j / \bar{B}_j \tag{3}$$

where C_j is catch of age j fish, and B_j is mean biomass. Mean biomass was approximated by

$$\bar{B}_j = (B_j + B_j + 1) / 2 \tag{4}$$

The iterative process is as follows: initially, fishing mortality rates of 0 are input to the dynamic pool model, and biomasses are estimated (allocated). Esti-

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[4] See footnote 2

TABLE 1

Dynamic Pool Model of Jack Mackerel Population and Estimates of Potential Yield, Using Assumed Schedule of Natural Mortality Rates

Age	Assumed natural mortality rate	Fishing mortality rate	Relative number	Length (mm-FL)	Mean weight[1] (g)	Initial biomass (10^3 MT)	Mean catch[2] (10^3 MT)	Potential yield (10^3 MT) Low $X=0.3$	Potential yield (10^3 MT) High $X=0.5$
0	(0.5)	—	1,000	—	—	—	—	—	—
0.5[3]	(0.5)	0.018	779	—	60	(123.3)	2.360	9.3[4]	15.4[4]
1	0.5	0.043	602	198	85	135.0	5.728	20.2	33.7
2	0.45	0.046	350	234	140	129.3	5.664	17.4	29.1
3	0.4	0.058	213	267	207	116.5	6.340	14.0	23.3
4	0.35	0.032	135	297	285	101.2	3.024	10.6	17.7
5	0.3	0.012	92	324	370	89.7	1.048	8.1	13.4
6	0.25	0.004	67	349	461	81.8	0.337	6.2	10.3
7	0.2	0.002	52	372	556	76.6	0.124	4.6	7.6
8	0.2	0.001	43	392	653	73.5	0.025	4.4	7.3
0-8	—	—	—	—	—	926.8	24.649	94.8	157.9
9-15	0.2	—	145	411-493	959	367.0	—	22.0	36.7
16-30	0.2	—	45	503-576	1598	190.3	—	11.4	19.1
0-30						1360.8 (spawning) 1484.1 (total)		128.3	213.7

[1] Weight is based on length-weight relationship with correction for $\sigma_L = 21.5$ mm (Pienaar and Ricker 1968)

[2] Catch includes only San Pedro landings.

[3] Age O fish are assumed to be unavailable for the first half year; mean weight is approximate; and biomass does not spawn.

[4] Potential yield reduced by ½ because fish are only available for ½ year.

mates of F_j are then made by equations (3) and (4), given the mean catch of fish at age for the 1952-53 through 1971-72 fishing seasons (Fleming and Knaggs 1977). These fishing mortality rates are then used in the dynamic pool model to produce new biomass estimates for the second iteration. The estimates of F converge to two significant digits with three iterations.

Estimates of F are given in Tables 1 and 2 and reflect a southern California fishery of approximately 24,649 MT per year, which is the average San Pedro catch for the 1952-71 period. Fishing mortality on older fish caused by incidental catches and the foreign trawl fishery has been ignored, because of lack of information on magnitude and age composition. Recent foreign trawl catches are up to 2,000 tons per year, but the 1952-71 average is much smaller—not large enough to significantly affect the model.

The potential yield estimator of Gulland (1970) is intended to provide a reasonable limit to exploratory expansion of a fishery. It is not meant to be an esti-

TABLE 2

Dynamic Pool Model of Jack Mackerel Population and Estimates of Potential Yield, Using Assumed Natural Mortality Rates and Partial Fecundity of Young Fish

Age	Assumed fecundity	Assumed natural mortality rate	Fishing mortality rate	Initial biomass (10^3 MT)	Potential yield (10^3 MT) $X=0.3$	Potential yield (10^3 MT) $X=0.5$
0.5[1]	0	(0.5)	0.032	(148.2)	11.2[2]	18.5[2]
1	0.2	0.5	0.036	161.0	24.1	40.3
2	0.4	0.45	0.038	155.1	21.0	34.9
3	0.6	0.4	0.048	140.9	16.9	28.2
4	0.8	0.35	0.026	123.6	13.0	21.6
5	1.0	0.3	0.010	110.3	9.9	16.5
6	1.0	0.25	0.003	100.8	7.5	12.6
7	1.0	0.2	0.001	94.3	5.6	9.4
8	1.0	0.2	0.001	90.6	5.4	9.1
0-8	—	—	—	1124.9	114.6	191.1
9-15	1.0	0.2	—	452.5	27.1	45.3
16-30	1.0	0.2	—	234.6	14.1	23.5
0-30				1360.8 (spawning) 1812.0 (total)	155.8	259.9

[1] Age 0 fish are assumed to be unavailable for the first half year; mean weight is approximate; and biomass does not spawn

[2] Potential yield reduced by ½ because fish are only available for ½ year

mate of maximum sustainable yield (MSY), but is an interim limit to catches while data sufficient to estimate MSY are being accumulated. Thus Gulland's estimator should not be treated as a goal for fishery development. In some cases it may be considerably in excess of true MSY, but we cannot know for the case of the jack mackerel fishery until more information is gained.

The potential yield estimator is given by

$$Y_{\text{pot}} = X\, M\, \bar{B}_0 \qquad (5)$$

where Y_{pot} is potential yield; M is natural mortality rate; $\bar{B}_0$ is mean virgin biomass; and X is a coefficient based on M, on Von Bertalanffy growth parameter K, and on c, the ratio of length at first capture to asymptotic length. The present biomass is only very lightly fished, and can be used for $\bar{B}_0$. A value of $X = 0.5$ is commonly used and will be used here for a "high" estimate. The value obtained from Gulland (1970) for $M/K = 2.5$ to 5.0, and relative length at first capture $c = 0.3$, is $X = 0.3$, providing a "low" estimate of potential yield. Gulland's estimator assumes a constant mortality rate, but M varies with age in the dynamic pool model. Therefore, the Gulland estimator is applied to each age separately, and potential yields are summed afterward (Tables 1 and 2).

The sensitivity of potential yield estimates to different assumed rates of natural mortality is somewhat different than sensitivity of biomass estimates. For the large-fish segment, decreases in natural mortality rate (M) result in offsetting increases in estimated biomass ($\bar{B}_0$), making potential yield estimates relatively constant (cf. equation 5). However, the sensitivity is compounded for the small-fish segment, where decreased overall rates of mortality result in a decreased portion of the total biomass being allocated to the small-fish segment, and potential yield drops considerably. Without good estimates of biomass and mortality rates, these estimates of potential yield must remain only tentative. Other estimates of potential yield, based on alternative mortality rate schedules and other assumptions, are given by MacCall et al. (1980).

Potential yield is estimated for three segments of the resource. Ages 0.5 through 8 represent the inshore small-fish fishery, and have a potential yield of about 100 to 200 thousand MT. The historical fishery has exploited fish aged 1 through 4 years more heavily than the other ages in the small-fish fishery. Based on yield-per-recruit considerations, there would be no detriment in obtaining an equivalent total yield from younger fish (e.g., ages 1-4) rather than in proportion to their biomasses over the entire range of ages. This argument does not extend to the large-fish segment, which is harvested independently. Potential yield of large fish ranges from 10 to 25 thousand MT. The intermediate group of ages 9 to 15 years has a potential yield of 20 to 50 thousand MT. The total stock has a potential yield of 130 to 260 thousand MT.

COMPARISON WITH OTHER *TRACHURUS* FISHERIES

The world catch of *Trachurus* is composed of about 13 species from the Atlantic, Pacific, and Indian oceans, and Mediterranean Sea (Berry and Cohen 1972). Two or more species often co-occur in the same region (e.g., Stephenson and Robertson 1977). In these cases one species typically attains a maximum size of 60-70 cm, and the other reaches a size of 40-45 cm. The smaller species is usually a coastal pelagic schooling fish vulnerable to purse seine fisheries. The larger species tends to be distributed widely offshore, forming semidemersal or pelagic schools, which are caught by bottom or midwater trawls. *Trachurus symmetricus* is the sole inhabitor of the northeast Pacific, and appears to fill both of these ecological niches.

Except for growth, population parameters are poorly known for most stocks of *Trachurus*. Rates of growth are relatively slow. Age at first maturity ranges from 1 to 4 years. Longevity varies from 6 years for *T. japonicus* to 35 years for *T. trachurus* (Macer 1977), the latter value being similar to that for *T. symmetricus*. Differences in longevity can be attributed to differences in age determination techniques and exploitation rates as well as inherent differences among species. Stock abundance, recruitment, and mortality rates have not been estimated for any of the *Trachurus* stocks, making *T. symmetricus* among the best-known cases. Fisheries on these stocks have developed with very little management information on their status or potential yield.

The total world landings of *Trachurus* have increased in the last 20 years from about 0.9 to 2.7 million MT in 1980 (Table 3). The major fisheries occur along the eastern Atlantic from the English Channel to South Africa; the total annual Atlantic harvest has exceeded 1 million MT since 1971, although some fisheries such as *T. trachurus capensis* off South Africa have declined severely. The large fishery off Japan has declined steadily from 0.6 million MT in 1965 to 0.06 million MT in 1980. This decline suggests that the stock was overfished, but has not collapsed catastrophically. The South American fishery off the coasts of Peru and Chile has increased rapidly since the collapse of the Peruvian anchoveta fishery in 1972, although the extent to which stock abundance or productivity has increased is unknown. The South American catch has exceeded 1 million MT since 1978, and accounts for all of the recent increase in

TABLE 3

World Catch of *Trachurus* spp by Oceanic Regions for 1965 to 1980 in 1,000 MT[1]

	Atlantic Ocean				Pacific Ocean					
	North eastern	Central eastern	South eastern[2]	Medit. Sea	North western	South western	North eastern	South eastern	Indian Ocean	Total
1965	124	52	311	42	553	—	30	15	—	1,127
1966	109	37	300	41	487	<1	19	22	—	1,015
1967	119	102	245	62	334	<1	17	30	—	909
1968	143	166	206	43	315	<1	25	27	—	925
1969	152	258	148	42	286	<1	24	23	—	969
1970	249	297	232	37	222	<1	22	117	—	1,176
1971	241	480	384	42	283	14	27	168	<1	1,639
1972	260	456	363	56	156	19	24	180	<1	1,514
1973	356	486	482	65	131	16	9	164	3	1,712
1974	285	501	346	43	169	19	10	324	4	1,700
1975	277	444	444	45	193	14	17	299	5	1,738
1976	354	433	679	64	138	16	18	377	5	2,084
1977	224	492	753	64	95	18	50	848	35	2,579
1978	146	330	968	76	64	11	32	1,025	10	2,662
1979	143	250	768	118	93	8	17	1,287	8	2,692
1980	137	490	695	94	57	7	22	1,195	35	2,732

[1] Source is FAO catch statistics.

[2] Includes a few tons from southwestern Atlantic off South America.

world catch of *Trachurus*. *Trachurus symmetricus* off California, and the New Zealand and Indian Ocean species appear to be the only remaining lightly exploited *Trachurus* stocks.

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GROWTH OF THE BLUE ROCKFISH *(SEBASTES MYSTINUS)*

JOHN S. MACGREGOR
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038

ABSTRACT

Weight-length and age-length data were obtained for samples of blue rockfish (*Sebastes mystinus*) taken off southern California.

For weight-length, $W = aL^b$, the value of a was found to be 2.043×10^{-5}; the value of b, 3.059.

The Von Bertalanffy curve was used for age length. It was determined that $L_\infty = 327.6$ mm, $k = 0.1428$, and $t_0 = -1.553$.

RESUMEN

Colecciones de *Sebastes mystinus* obtenidas en la región meridional de California, han proporcionado los datos básicos para establecer las relaciones entre peso y longitud, así como entre edad y longitud.

Para la relación peso y longitud, $W = aL^b$, se obtuvo el valor resultante 2.043×10^{-5}; siendo $b = 3.059$.

La curva de von Bertalanffy se utilizó para la relación edad y longitud. Así se ha determinado que $L_\infty = 327.6$mm, $k = 0.1428$, y $t_0 = -1.553$.

INTRODUCTION

The blue rockfish, *Sebastes mystinus*, is an important sport fish along the California coast, especially in central and northern California, where it was the most abundant species taken by hook-and-line fishermen in a 1957-61 survey (Miller and Geibel 1973). In the central California partyboat fishery, blue rockfish accounted for 27% of the total catch of all species and 31% of the rockfish catch.

The blue rockfish is less important in the southern California sport catch. In this area the sport fishery relies more on migratory surface species in summer and on rockfish during the winter when the other species are less available. In central California, although the blue rockfish are nonmigratory, the catch tends to be very low in the winter and high in the summer; Miller and Geibel (1973) attribute this to a seasonal change in feeding habits.

The purpose of this paper is to present growth data on blue rockfish off southern California. Such data are necessary to an understanding of the life history and population dynamics of the species. A secondary purpose is to compare and contrast these data with other published data on the blue rockfish.

MATERIALS AND METHODS

Blue rockfish were caught on hook and line off southern California (Table 1). Standard length, fork length, total length, and weight were obtained for each fish. Otolith and scale samples were taken.

Scales were used for aging the blue rockfish because they appeared to be easier to read than otoliths and also because it is much more convenient to back-calculate lengths from scales. In addition, *Sebastes* species tend to exhibit nonisometric growth of otoliths. For a 130-mm fish the otolith equals 5.4% of standard length, whereas for a 330-mm fish it equals only 4.1% of standard length. This further complicates back-calculating lengths from otoliths.

There is no good way to verify isometric growth of rockfish scales relative to length. We assume that growth is isometric primarily because the scales and scale pockets are integral parts of the covering of the fish's body. One objection raised to back calculations of length from scale annuli is that the scales do not begin to form until the rockfish are about 15 mm long. However, when the scale does form, it forms as a plate and not as a point.

In many fishes, especially temperate freshwater species, the scale annuli are formed by a change in spacing of circuli. The circuli are more widely spaced when water temperatures, feeding, and metabolism are high, and more closely spaced when these factors are low.

In many species of saltwater fishes, annuli consist

TABLE 1
Blue rockfish Caught Off Southern California

			Standard length (mm)	
Locality	Date	Number	Mean	Range
Bird Rock (La Jolla)	1-25-78	4	165	156-179
San Nicolas Island	5-31-79	35	252	193-301
San Nicolas Island	9-07-79	20	231	190-290
Santa Barbara Island	5-31-79	11	220	172-283
San Clemente Island	9-06-78	9	221	147-308
San Clemente Island	5-29-79	1	235	
San Clemente Island	8-09-79	3	195	180-223
Osborne Bank	8-04-71	2	256	252-259
Tanner Bank	3-1-77	10	271	260-286
Tanner Bank	9-07-78	12	275	233-325
Cortes Bank	5-30-79	12	221	162-266
Cortes Bank	9-05-79	5	200	172-248
		124		147-325

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of bands of broken circuli. These are especially noticeable in species with a marked fat cycle, such as the California sardine, *Sardinops sagax (S. caeruleus).* The sardine gains weight during the summer and loses weight during the winter. A sardine taken in September might be 20% heavier than one of similar length taken in March.

The circuli on the scales of sardines are about equally spaced throughout the year. However, when the fish loses subcutaneous fat deposits during the winter, apparently the elastic skin tightens enough to exert pressure on the scale pockets. This causes an erosion and breaking of circuli around the edge of the scales. When the fish begins to gain weight and grow more rapidly in the spring, normal circuli are again laid down at the edge of the scale. All of the blue rockfish scales had checks caused by broken circuli.

Loss of scales can cause a change in scale-pocket tension on adjacent scales and result in false annuli being formed in the scales near the area of scale loss. These false annuli are often noticeably more or less prominent than the true annuli and also may be markedly asymmetrical, depending on their distance and direction from the area of scale loss. Sampling scales from several locations on both sides of the fish decreases the chance of obtaining scales with false annuli in similar positions relative to the scale center.

Rockfish scales tend to be deciduous. In some species it is almost impossible to find scales that are not regenerated, whereas in others only a small percentage of the scales are regenerated. Blue rockfish fall somewhere between the two extremes.

In sampling rockfish scales it is often useful to include lateral-line scales in the sample in case no other unregenerated scales can be found. These scales are seldom deciduous, but there is a tubelike structure in the center of each scale that generally obscures the first annulus and makes the center of the scale difficult to locate. Fortunately, the blue rockfish generally had enough unregenerated regular scales so that it was not necessary to rely on lateral-line scales for most of the fish sampled.

The scales were mounted dry between two microscope slides and projected on a sheet of white paper at about 30× to 50× magnification. The scale center, annuli, and scale margin were marked for the six best scales for each fish. I obtained back-calculated lengths for each of the six scales and compared the readings to determine the age and average back-calculated lengths.

Annuli were considered valid if they appeared in the approximate same location in at least four of the six scales. The average value was obtained for each of the sets of readings to arrive at length at age for each fish.

LENGTH-WEIGHT RELATIONSHIP

Length and weight data were obtained from 98 blue rockfish ranging from 147 to 325 mm in standard length.

The usual formula describing a length-weight curve for fishes is $W = aL^b$. This may be obtained by transforming the straight line, $\log W = \log a + b \log L$, or directly by nonlinear methods (Marquardt's least squares) (Figure 1). The former should give the best least-squares fit to the logs of length and weight; the latter should give the best fit to the arithmetic curve. If the values of b are close to 3, the formula $W = aL^3$ may be used in which $a = K$; ($K = W/L^3$).

The values of a and b for the three curves are:

nonlinear $a = 2.04262 \times 10^{-5}$ $b = 3.05934$
log log $a = 2.12486 \times 10^{-5}$ $b = 3.05240$
cubic $a = 2.82587 \times 10^{-5}$ $b = 3.00000$

The calculated values of weight are the same between lengths 20 and 340 mm for the nonlinear and log log curves. The weights calculated from the cubic curve are slightly higher than those for the other two curves for lengths up to 240 mm, and slightly lower above 240 mm (Table 2).

The residuals from the nonlinear fit (Figure 2) increase with increasing length. An arithmetic standard error of estimate is useless for determining limits of weight divisions. There is no increase in residuals of log weight with log length. For the curve, $\log W = -4.67267 + 3.05240 \log L$, $Sy = 0.038498$. This value of S_y may be applied to the arithmetic curve as a

TABLE 2
Calculated Weights (grams) for Blue Rockfish

	Southern California		Monterey[a]		
Standard length (mm)	Male & female	Male & female	Female	Male	Male & female
20	0.20	0.23	0.37	0.22	0.73
40	1.65	1.81	2.60	1.72	4.27
60	5.69	6.10	8.11	5.77	12.0
80	13.7	14.5	18.2	13.6	24.8
100	27.1	28.3	34.1	26.6	43.7
120	47.2	48.8	56.8	45.8	69.3
140	75.5	77.5	87.6	72.6	103
160	111	116	127	108	144
180	163	165	177	154	194
200	224	226	238	211	253
220	300	301	311	280	322
240	391	391	397	363	402
260	500	497	498	462	492
280	627	620	613	576	594
300	774	763	744	708	708
320	942	926	892	858	834
340	1133	1111	1058	1029	972
Number of fish	98	98	147	58	278
Log a	−4.67267	−4.54885	−4.8346	−4.55299	−3.43180
b	3.05240	3.00000	2.80779	2.98849	2.53589

(a) Miller and Geibel 1973.

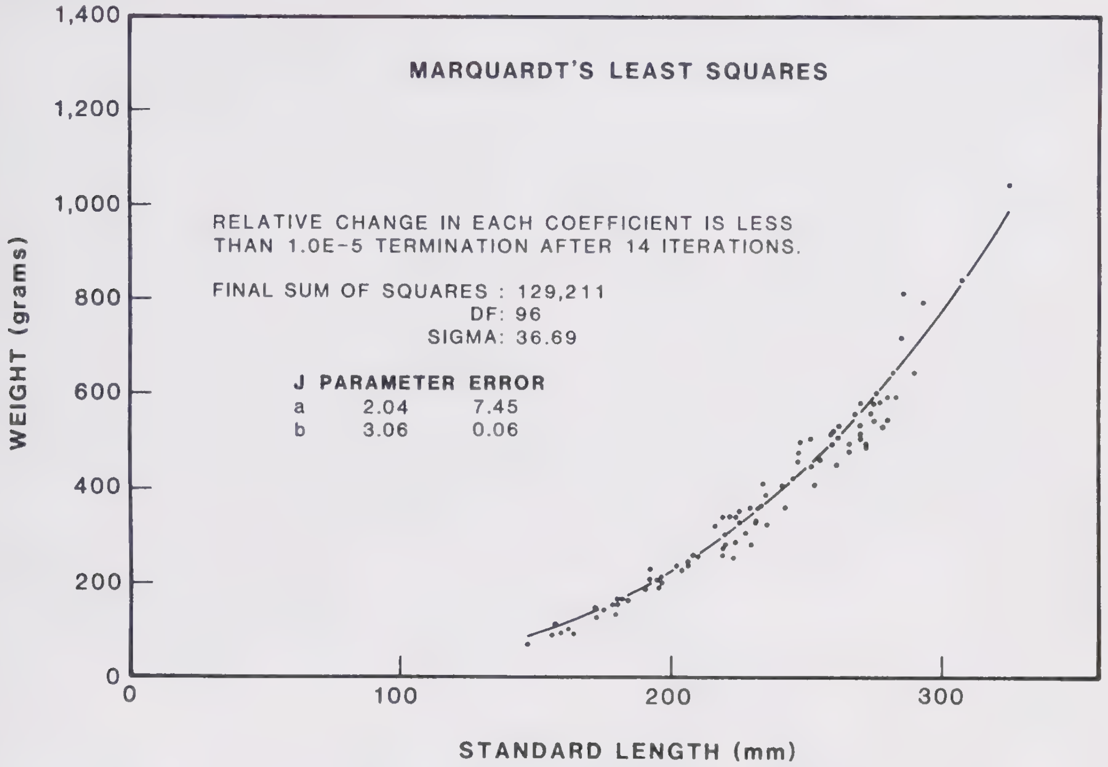


Figure 1. Length-weight curve ($L = 2.045W^{3.059}$) for blue rockfish taken off southern California.

percentage: $S_y = +9.27\%, -8.48\%$; $2S_y = +19.39\%, -16.24\%$.

Miller and Geibel (1973) give length-weight formulas that they obtained for blue rockfish from the Monterey area. Their data were collected in total length in mm and weight in pounds. We have converted these formulas to standard length and grams for comparison ($SL = 0.8127\ TL$) (Table 2).

They also give length-weight curves for male fish, females, and sexes combined. The females do give a slightly higher curve, but this is probably fortuitous. When they added 73 apparently unsexed fish to get a combined curve, they obtained values higher than either the male- or female-only curves. However, the curves all agree well with that based on the data from this study (Figure 3).

AGE-LENGTH RELATIONSHIP

We were unable to get samples of young fish to obtain length-frequency data that could establish the ages of these fish. Wales (1952) and Miller and Geibel (1973) obtained samples of juvenile blue rockfish from the Monterey area; we have compared these with average observed lengths back-calculated from scales for younger blue rockfish from southern California (Table 3).

The data of Wales (who used fork length) and Miller and Geibel (who used total length) were converted to standard length by the formulas $SL = 0.8506\ FL$ ($\sigma = 0.0069$) and $SL = 0.8127\ TL$ ($\sigma = 0.0091$). These formulas were based on measurements from fish 147 mm SL and larger and may not be entirely applicable to the smaller fish. The agreement with Wales's data seems to be very good. Miller and Geibel's samples show little growth in the second year, but this may be because larger fish migrate out of the nursery area to deeper waters.

The Von Bertalanffy growth curve is widely used to describe fish growth. The equation takes the form:

$$L_t = L_\infty\,(1 - e^{-k(t\ -\ t_0})\,)$$

There are several methods of solving the equation. The values of L_∞, k and t_0 may be obtained from two simple equations of the $Y = a + bX$ type.

In the first equation X equals length at age t (L_t), and Y equals length at age $t + 1$ ($L_t + 1$) (Figure 4.)

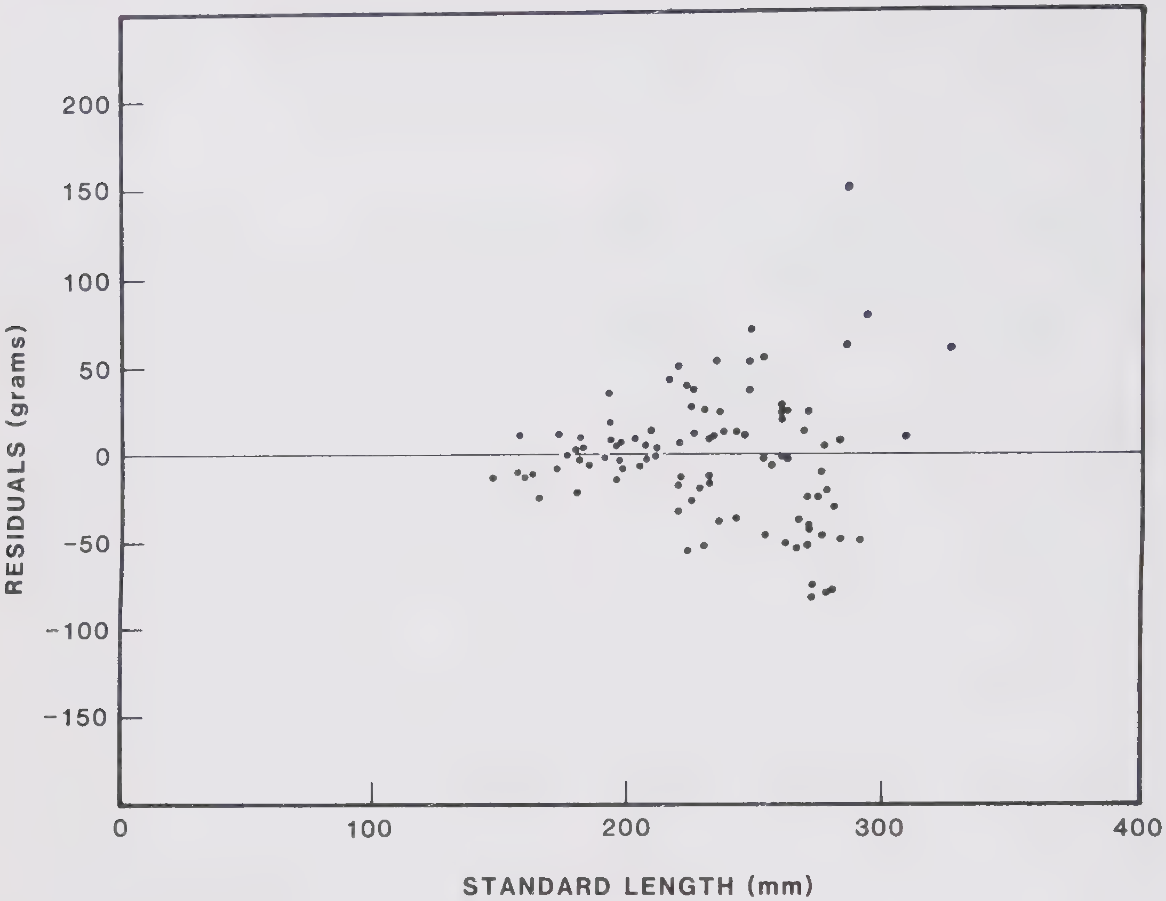


Figure 2. Residuals (L_o-L_c) of length-weight curve for southern California rockfish.

Length at infinity (L_∞) is assumed to be the point at which the computed line intersects the 45° diagonal from the origin. The value of k is obtained from $k = \log_e{}^{1/b}$. It is obvious from the angle at which the computed line intersects the diagonal that little variation around the line would take in a considerable range of lengths at age at infinity.

In the second equation X equals age, and Y equals $\log_e (L_\infty - L_t)$ (Figure 5). The value of t_0 (age at length zero) is obtained from $t_0 = a - \mathrm{Log}_e L_\infty / K$.

The second equation, when plotted, gives a good visual representation of the final age-length fit. Ricker (1958) suggests adjusting this equation to obtain a better fit by using trial values of L_∞, that is, iterating to get a better value of L_∞ for the Von Bertalanffy equation.

We have arbitrarily obtained two additional estimates of L_∞ by recalculating the first equation omitting the first pair of values (L_1 and L_2) from one equation and the second pair (L_2 and L_3) from the other. Both of these increase the value of L_∞. Length at infinity equals 313, 336, and 362 for the 12, 11, and 10 pairs of values, respectively.

Calculated values of length are closer to observed values for the second (336 mm) and third (362 mm) values of L_∞ than for the first (313) (Table 4). The sum of the squares of deviations of calculated length from observed length for the 12 pairs of values for the first value of L_∞ is 320; for the second, 128; and for the third, 284.

These equations can be used instead of the Von Bertalanffy equation to get the same calculated lengths and without the necessity of obtaining k and t_0. The equation $\log_e (L_\infty - L_t) = a + bt$ (in which t equals age) can be changed to $L_t = L_\infty - e^{(a + bt)}$, which also is easier to use than the Von Bertalanffy equation.

TABLE 3
Length-Frequency Data Used to Estimate Length at Age for Juvenile Blue Rockfish

			Monterey	
Month	Age	Southern California	Wales	Miller and Geibel
April				41 (one fish)
June				57 mean
July			58-65 = Range	56 mean
Aug.				58 mean
Sept.				62 mean
Oct.				65 mean
Nov.				69 mean
Dec.				70 mean
Jan.				73 mean
Mar.	1	95		80 mean
Apr.				83 mean
May				88 mean
June			96-126 = Range (115 = mean)	
July				87 mean
Aug.				99 mean
Sept.				
March	2	133		
June			mean = 149	
March	3	163		
June			mean = 170	
March	4	181		

Monterey in 1929-30 (Wales 1952) and the 1964 year class in 1964-65 (Miller and Geibel 1973) compared with observed lengths back calculated from scales for southern California. All lengths are standard lengths in mm.

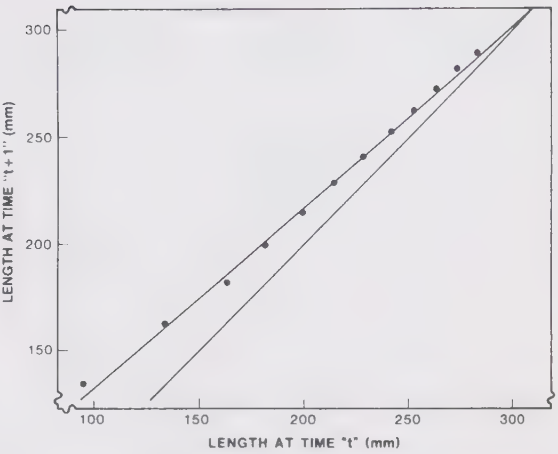


Figure 4. Plot of length at age plus one against length at age with the calculated regression line for blue rockfish.

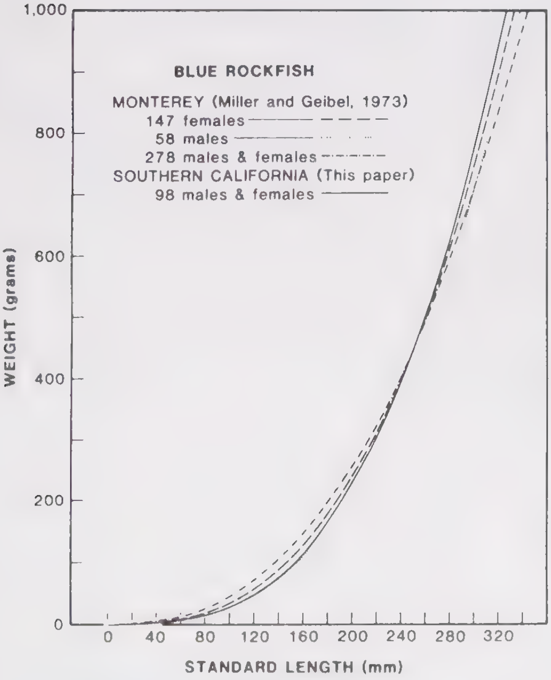


Figure 3. Comparison of blue rockfish length-weight curves, southern California and Monterey (Miller and Geibel 1973).

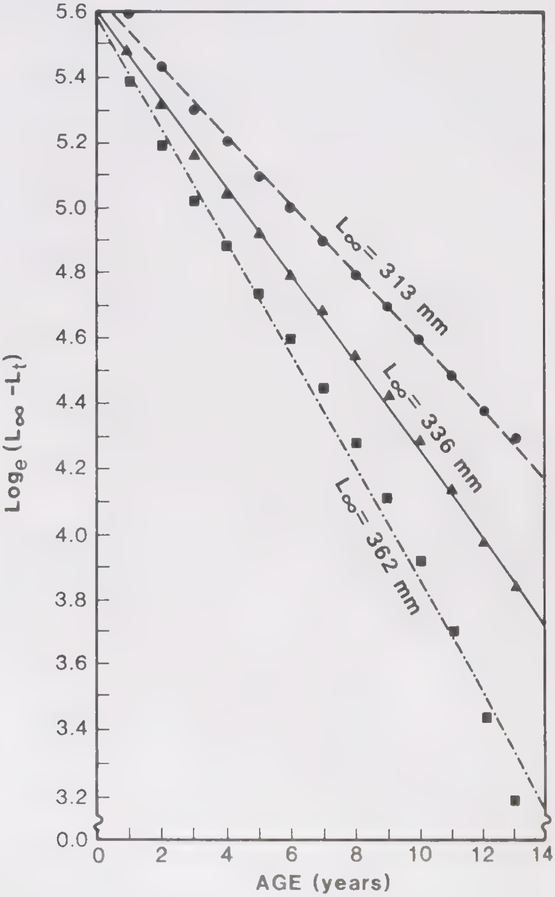


Figure 5. Plots of $\log_e (L_\infty - L_t)$ against age for blue rockfish

In the Von Bertalanffy equation for the blue rockfish $k = 0.1316$ and $t_0 = -1.738$ for $L_\infty = 336$.

Tomlinson and Abramson (1961) give a method of fitting a Von Bertalanffy curve by least squares. Using this method, a value of 327.3 mm is obtained for L_∞; 0.1430 for k; and -1.5487 for t_0. The sum of d^2 is 118.

TABLE 4

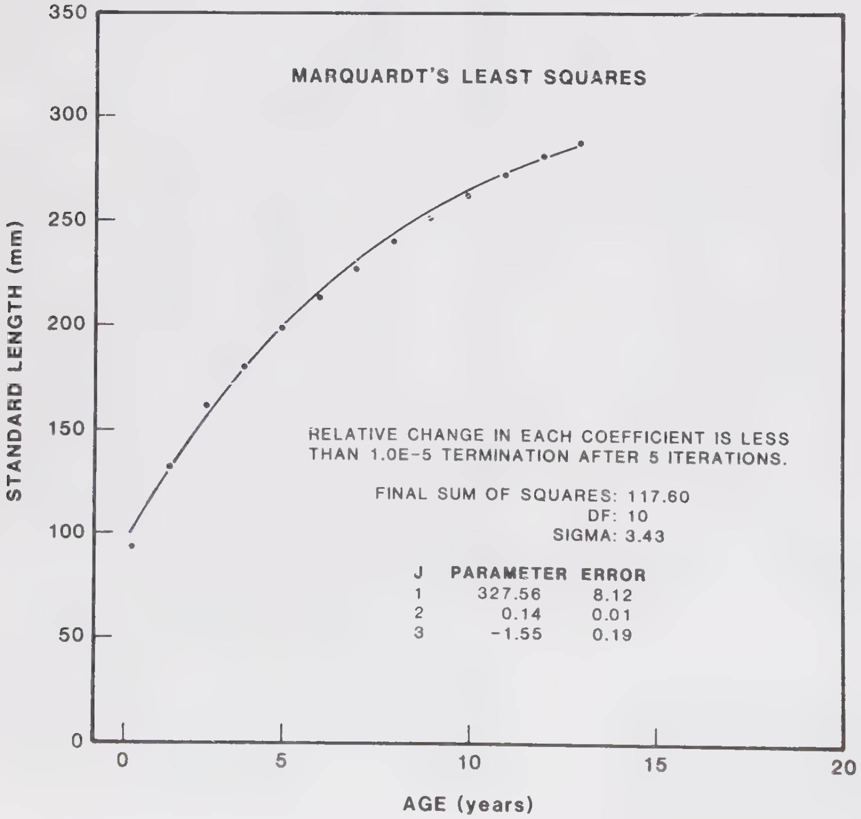
Computed Values of Length at Age for Blue Rockfish: $L_t = L_\infty - e^{(a + bt)}$.

Age	Observed length	Calculated length		
		$L_\infty = 313$	$L_\infty = 336$	$L_\infty = 362$
1	94.5	87.1	101.8	109.3
2	113.4	123.3	130.8	134.4
3	162.5	153.7	156.2	157.1
4	181.4	179.3	178.4	177.5
5	199.5	201.3	197.9	195.9
6	214.4	218.8	215.0	212.5
7	228.1	233.9	230.0	227.4
8	241.3	246.6	243.1	240.8
9	252.5	257.3	254.6	252.9
10	263.1	266.3	264.7	263.8
11	273.2	273.8	273.5	273.6
12	282.5	280.2	281.2	282.4
13	289.1	285.5	288.0	290.4
	$a =$	5.59644	5.58816	5.63799
	$b =$	−0.17437	−0.13225	−0.10488
	$\Sigma d^2 =$	374.84	128.47	284.20

Using a Marquardt nonlinear least squares computer program to minimize the sum of d^2 by iteration from estimated values, 327.6 mm is obtained for the value of L_∞; 0.1428 for k; and -1.5535 for t_0 (Figure 6).

All of the above curves are based on average lengths at each age. A nonlinear least squares curve based on all length measurements at each age was also calculated (Figure 7). This weights the curve to those lengths for which there is most data. When back-calculated lengths are used, this means that the curve is weighted more heavily to the lengths at younger ages. It would appear that fewer older fish are more representative of their true size at age than lengths influenced by extrapolations of the more heavily weighted younger fish (Table 5). The value of L_∞ for the weighted curve is 313.0 mm; of k, 0.1600; and t_0, -1.3696.

The standard error of estimate for the weighted curve is 18.6 mm. However, the residuals (Figure 8)



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RELATIVE CHANGE IN EACH COEFFICIENT IS LESS
THAN 1.0E-5 TERMINATION AFTER 5 ITERATIONS.

        FINAL SUM OF SQUARES: 117.60
                             DF: 10
                         SIGMA: 3.43

   J  PARAMETER  ERROR
   1     327.56   8.12
   2       0.14   0.01
   3      -1.55   0.19
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Figure 6. Von Bertalanffy length-age curve using mean lengths at age for blue rockfish.

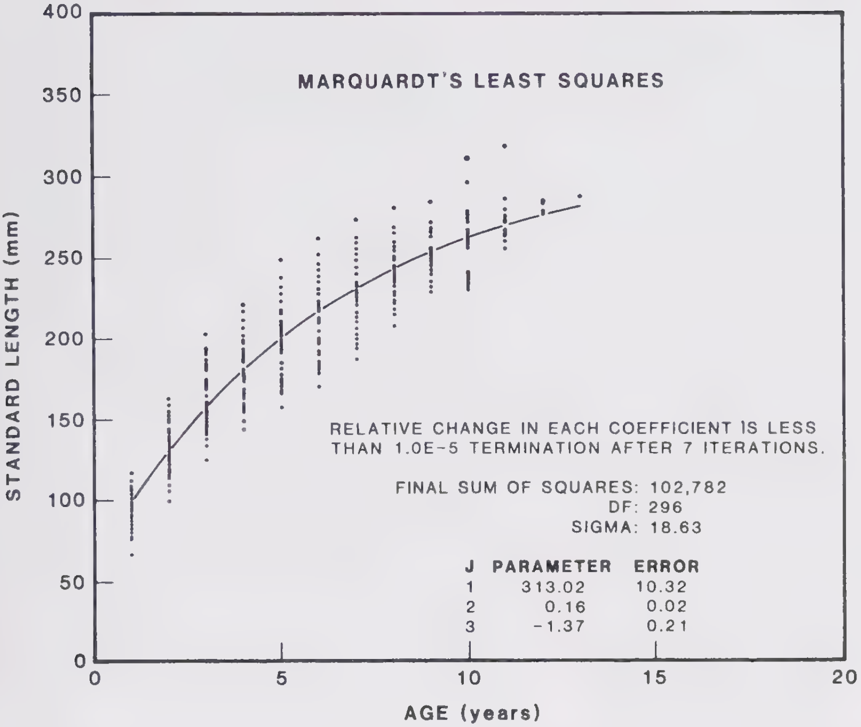

Figure 7. Von Bertalanffy length-age curve using sample of 299 age readings for blue rockfish (28 readings, age 1 through 10; 14 readings, age 11; 4 readings, age 12; 1 reading, age 13).

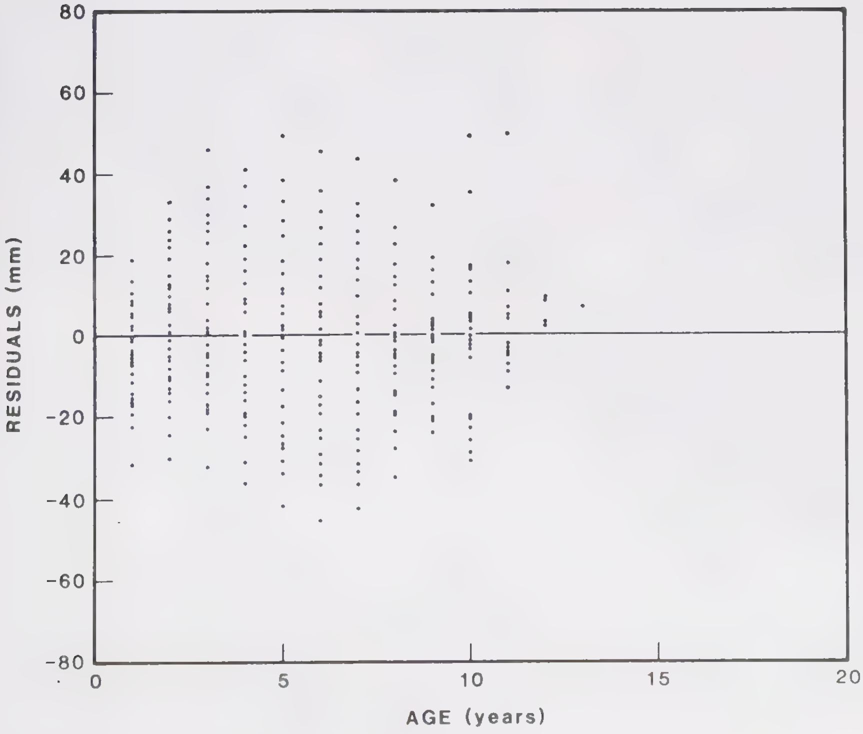

Figure 8. Residuals ($L_o - L_c$) of length-age curve for blue rockfish

TABLE 5

Standard Lengths (mm) at Age for Various Calculations of the Von Bertalanffy Growth Curve Compared to Back-calculated Observed Length for Blue Rockfish

Age (years)	Observed length (mm)	Standard length (mm)					
		Trial values of $L\infty$ Ricker (1958)			Least squares Tomlinson and Abramson (1961)	Marquardt	
						Unweighted	Weighted
1	95	87	102	109	100	100	99
2	133	123	131	134	130	130	130
3	163	154	156	157	157	157	157
4	181	179	178	178	179	179	180
5	200	201	198	196	199	199	200
6	214	219	215	213	216	216	216
7	228	234	230	227	231	231	231
8	241	247	243	241	244	244	243
9	253	257	255	253	255	255	253
10	263	266	265	264	265	265	262
11	273	274	274	274	273	273	270
12	283	280	281	282	280	280	276
13	289	286	288	290	286	286	282
	Length at Infinity =	313	336	362	327.3	327.6	313.0
	k =		−0.132		−0.1430	0.1428	0.1600
	t_0 =		−1.738		−1.549	−1.553	−1.370

increase in error to age six, followed by a decrease. If we calculate standard deviations for each age using the nonlinear curve value as a "mean" we obtain:

Age	σ	*Age*	σ
1	12.6	7	23.0
2	17.0	8	16.8
3	20.9	9	12.3
4	20.3	10	17.9
5	23.2	11	16.3
6	23.5	12	8.1

I have used the unweighted nonlinear curve values for further comparison with the data of Miller and Geibel (1973). They computed a Von Bertalanffy curve for their age-length data based on scale readings, but they do not give values for either the parameters of the curve or their age-length data. We have picked approximate values from their figured curve for combined sexes and have recomputed the age-length curve to compare with our data (Table 5, Figure 9). Their values are lower than ours for the first few years but eventually catch up.

The biggest difference is in the first year's growth in which the average back-calculated length attained by southern California fish is 95 mm, and by Miller and Geibel's Monterey fish only 75 mm. For the next 5 years the growth increments of the Monterey specimens are slightly greater until, at age seven, fish from both areas are approximately the same length.

We did not take any samples of mature blue rockfish during the winter and, therefore, could not delimit

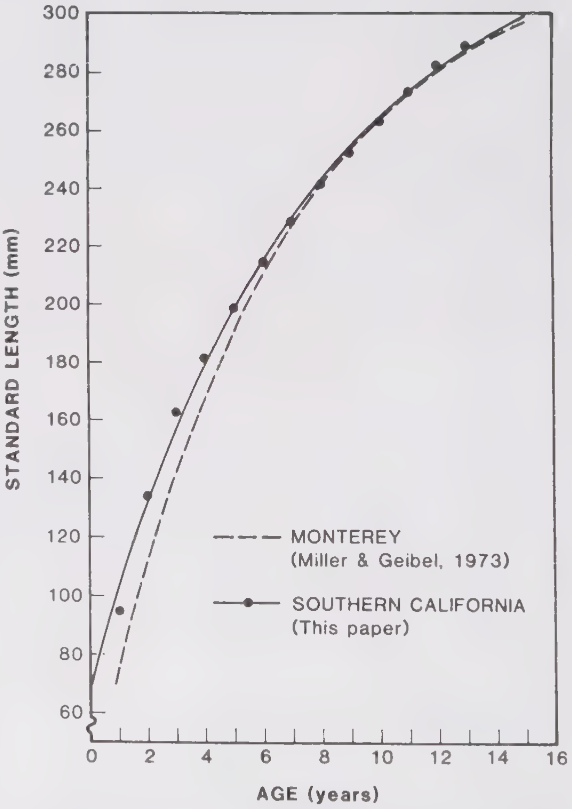

Figure 9. Comparison of length-age curves, blue rockfish, southern California and Monterey (Miller and Geibel 1973).

the spawning season off southern California. Wales (1952) states that spawning took place in the Monterey area in November, December, and January. Miller and Geibel (1973) found that annuli are formed in March and April. Because annuli do not form on the scales when the fish are only a few months old, the first annulus may be formed when the fish is one year and three months old and the second approximately a year later at age two years and three months. Thus the first "year" may be longer or shorter than a year for different species of fishes, depending on when annulus formation occurs in relation to the spawning season.

This phenomenon is more marked in some species. Sardines in the northern part of their range tended to spawn later than those off southern California and northern Mexico, and showed apparent slow growth (i.e., a shorter first year) in length at age one back-calculated from scales. However, they grew much faster than the more southerly populations of sardines in subsequent years and soon outgrew them.

Actually, although the blue rockfish probably have a long first "year", their first year's growth appears to be less than a year's growth compared with the best-fitting curves that we computed. However, 9 of 10 species of rockfish show negative deviations of observed values from Von Bertalanffy curves for the first year in Phillips's (1964) data (Table 6).

Considering the possible variation that one might expect, the pattern of deviations in Phillips's data is noteworthy. From the second to fifth year the observed values tend to be higher than computed values; from the sixth to eleventh year they tend to be lower; and from the twelfth on, higher (Table 6). For the blue rockfish the pattern is remarkably similar.

One possible explanation of this is that male rockfish of many if not all species tend to be slower growing and shorter lived than females. For the first few years the fish grow more rapidly, and there is less difference in growth rates between the two sexes (plus deviations) until sexual maturity is reached. Then, for several years, the slower growth of the males causes the curve to dip (minus deviations). The increasing higher mortality of the slower-growing males in the later years gradually increases the proportion of faster-growing females in the population causing a final rise in the curve (plus deviations).

CONCLUSIONS

The length-weight data for blue rockfish from southern California show nearly isometric growth. Therefore the formula $W = KL^3$ may be used instead of $W = aL^b$.

The length-weight curve for southern California blue rockfish was close to the curves obtained by Miller and Geibel (1973) for samples from Monterey.

Several modifications of the Von Bertalanffy growth curve were used to describe the age-length relationship. Growth of southern California blue rockfish appeared to be more rapid than for Monterey samples for the first few years. This was caused by the smaller length at age one calculated for Monterey fish. Growth increments were actually greater for the following 5 years until they caught up with southern California fish.

There was a tendency toward a slight "S" shape to the curve of observed values of age length, which caused it to not quite fit the Von Bertalanffy curve. This tendency appears to hold true for other species of rockfishes also, and may be caused by differences in growth rates and mortality between male and female rockfish.

Conversions to standard length from fork length and total length (in millimeters) are: $SL = .8506FL$ and $SL = .8127TL$.

TABLE 6

Deviations of Observed Total Length from Von Bertalanffy Curve for Ten Species of Rockfish (Phillips 1964) Compared to Deviations (Standard Length) of Blue Rockfish from Southern California

Species of rockfish	Deviation at age													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Bocaccio	−4.4	+4.0	+4.4	+1.2	−3.0	−6.5	−2.4	+0.5	+2.4	+0.5	+2.4	+4.4	+3.2	+6.3
Chilipepper	−4.7	+2.7	+6.4	+5.3	−0.3	−5.8	−8.4	−7.1	−1.7	+2.2	+3.9	+6.0	+11.1	+16.8
Yellowtail	−1.0	−1.2	+1.0	+3.2	+3.7	+0.5	−3.5	−4.0	−5.8	−6.4	−4.5	+0.8	+5.8	+11.5
Dark blotched	+1.4	−1.6	−1.8	−0.4	+0.5	+2.8	+4.9	+0.1	−3.3	−4.8	−4.7	−2.4	−0.3	+9.3
Splitnose	−1.0	+1.4	+1.5	−0.3	−1.4	−0.3	+0.7	+0.3	−1.0	−1.2	+1.3	+0.4	+0.8	+1.5
Canary	−0.3	−1.8	0.0	+2.2	+2.2	+1.3	+0.8	−1.7	−4.7	−3.5	−1.7	−1.4	+7.1	+9.5
Vermilion	−4.5	+1.0	+4.5	+2.6	+3.0	−0.8	−3.2	−1.5	−0.9	−2.7	−5.2	−2.7	+2.8	+0.1
Widow	−0.1	−1.2	+0.2	+6.0	−0.1	−7.0	−6.4	−4.5	−1.4	+0.3	+2.6	+6.3	+8.7	+17.6
Stripetail	−2.9	+2.7	+2.2	+1.9	−0.9	−0.5	−0.4	−3.1	−4.7	−2.5	−0.9	0.0	+1.0	+2.9
Shortbelly	−0.1	+0.5	+0.8	0.0	−1.4	−2.2	−0.8	+3.0	+3.2	+3.3	—	—	—	—
Mean deviation	−1.8	+0.7	+1.9	+2.2	+0.2	−1.9	−1.9	−1.8	−1.8	−1.5	−0.8	+1.3	+4.5	+8.4
Blue rockfish	−7.3	+2.6	+6.3	+3.0	+1.6	−0.6	−1.9	−1.8	−2.1	−1.6	−0.3	+1.3	+1.1	—

ACKNOWLEDGMENTS

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YEAR-TO-YEAR FLUCTUATIONS OF THE CALIFORNIA COUNTERCURRENT AND EFFECTS ON MARINE ORGANISMS

DOUGLAS R. McLAIN
Pacific Environmental Group
Southwest Fisheries Center
National Marine Fisheries Service
P.O. Box 831
Monterey, California 93942

DAVID H. THOMAS
Marine Resources Region
California Department of Fish and Game
411 Burgess Drive
Menlo Park, California 94025

ABSTRACT

Interannual fluctuations of alongshore currents off California can be inferred from fluctuations of dynamic height at a nearshore, deepwater station in Monterey Bay (station H-3) and from sea level at coastal tide gages. Hydrographic data for the period 1969 to 1978 at station H-3 show anomalous depressions of the 8° to 12°C isotherms by as much as 100 m during some years. The depressions are associated with anomalous elevations of dynamic height and sea level, and appear to occur in a double wave, one in summer and a second the following fall or winter. The anomalous depressions are apparently caused by two processes: (1) a remote forcing caused by propagation of coastal trapped waves poleward from El Niño conditions in the tropics and (2) a local forcing caused by anomalously strong onshore Ekman transport.

By geostrophy, anomalous elevations of the sea surface along the coast are associated with anomalous increases in northward alongshore currents. These increases in northward flow have a variety of effects on marine organisms, including range extensions of plankton and anomalous shifts of salmon's migration routes.

RESUMEN

Las fluctuaciones anuales en las corrientes costeras de California pueden determinarse mediante los datos obtenidos de varias fuentes; la elevación dinámica cerca de la costa, información obtenida en la estación localizada en aguas profundas de la Bahía de Monterey (Estación H-3), y los mareógrafos costeros. Los datos hidrográficos correspondientes al período de 1969 a 1978 en la Estación H-3 indican que durante algunos años se produce un descenso de las isotermas de 8° y de 12°C hasta los 100 m. de profundidad. Estos descensos están asociados con elevaciones dinámicas anómalas y del nivel del mar, presentándose una ondulación doble, una onda para el verano y otra a continuación en otoño o invierno. Estos descensos anómalos son aparentemente el resultado de dos procesos, uno local, ocasionado por el transporte Ekman, fuerte y anómalo hacia la costa, y otro con la acción alejada de esta región y en relación con el fenómeno del Niño en el trópico, produciendo la propagación hacia el polo de las olas atrapadas en la zona costera.

Elevaciones geostróficas anómalas de la superficie del mar a lo largo de la costa, están asociadas con incrementos también anómalos en la progresión de las corrientes costeras hacia el norte. Estos aumentos en el flujo hacia el norte ocasionan diversos efectos en los organismos marinos, incluyendo la amplitud de distribución del plancton y cambios en las rutas migratorias del salmón.

INTRODUCTION

The major alongshore currents of the California coast are normally described as an offshore, southward flow—the California Current—and a nearshore, northward flow—the California Countercurrent. Similar coastal currents and countercurrents are found in other eastern boundary current regions such as off the west coasts of South America, northwest Africa, and southwest Africa. The nearshore current flows northward from Baja California throughout the year (Wooster and Reid 1963; Wickham 1975) to Vancouver Island (Ingraham 1967; Reed and Halpern 1976). In fall and winter, the countercurrent is strong and reaches to the surface, inshore of the California Current; the flow is then called the Davidson Current (Hickey 1979). During the summer, persistent northwesterly winds occur along the California coast and blow the surface water southward, covering the countercurrent, which remains as an undercurrent at depths of 200 to 500 m (Chelton 1982). The area influenced by the countercurrent extends up to 500 km offshore from the California coast at depths below 200 m and has been described as the California Undercurrent Domain because of its broad seaward extent under the California Current (Dodimead et al. 1963; Favorite et al. 1976).

This paper describes an index of low-frequency variations of the countercurrent, based on a 10-year time series of frequent hydrographic observations and calculations of dynamic height anomalies at a deep station in Monterey Bay, California. Sea-level, ship-of-opportunity XBT, and surface-drifter data are compared with the index for agreement with the hypothe-

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sized variations of flow of the countercurrent. Available biological data are examined for consistency with the flow index.

The fluctuations of the alongshore currents off California are as yet poorly understood but appear to have an important role in changes in distribution and abundance of a variety of marine species. Not only are the changes in currents themselves important in changing the distribution of pelagic organisms, but associated changes in the depth of the density structure may also be significantly related to changes in concentrations of dissolved nutrients and biological productivity. The intensity of upward transport of nutrients from below the thermocline by wind mixing changes markedly with changes in thermocline depth. Bernal (1981) and Chelton (1981) found that long-period variations of zooplankton in the California Current are correlated with fluctuations of temperature in the eastern tropical Pacific. They suggested that zooplankton variations may be related to variations of nutrients advected from the north by the California Current, combined with a reduction of upwelling of nutrients caused by increased thermocline depth. The occurrence off California of organisms of southern origin is also related to increases in water temperature that appear to be associated with increases in the transport of coastal countercurrents (Radovich 1961).

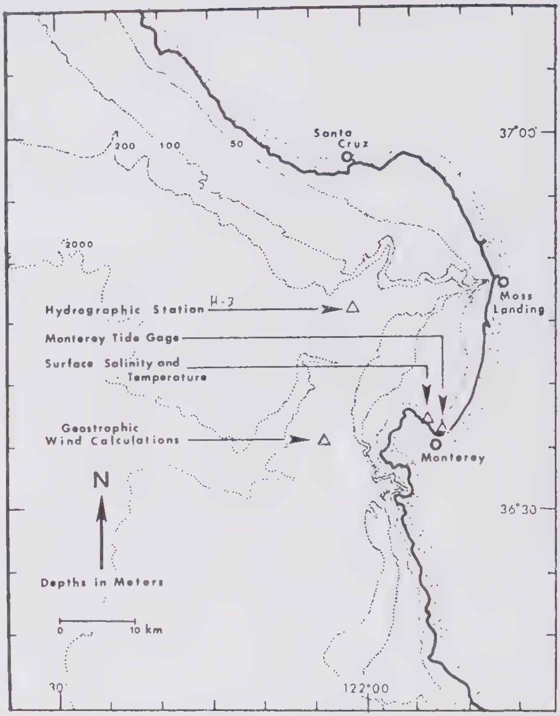

Figure 1. Map of the Monterey Bay, California, region showing location of data sources.

MONTEREY BAY HYDROGRAPHIC DATA

A unique set of time-series hydrographic observations is available in Monterey Bay, about 100 miles south of San Francisco (Bretschneider and McLain 1983). The data were collected at station H-3, located near the mouth of the Monterey submarine canyon, where water depth is more than 900 meters (Figure 1). Hydrographic observations in Monterey Bay were begun in the 1930s by Skogsberg (1936) and continued in the 1950s by Stanford University's Hopkins Marine Station (HMS) as part of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). The sampling program in Monterey Bay was designed to obtain more frequent monitoring of ocean fluctuations than was possible on large-scale CalCOFI surveys (Bolin and Abbott 1963). During the first years of the program, samples were collected at station H-3 to 100 m, but later sampling was limited to the upper 50 m of the water column. In 1968 the sampling depth was increased to over 500 m.[1] HMS sampling at H-3 ceased in December 1973, but sampling was continued at the same location by Moss Landing Marine Laboratories from July 1974 to June 1978 (station 2203).[2] In addition, several expendable bathythermograph (XBT) casts have been taken at nearly the same sampling location to depths of over 400 m by the Naval Postgraduate School, Monterey, California. Salinity values were estimated for each XBT profile so that XBT casts could be used to fill gaps in the time series of hydrographic stations (Bretschneider and McLain 1983). These data were merged to form a time series; 1968 data were deleted because their temperature-salinity curves appeared erratic. The final time series contains 241 hydrographic profiles taken in the 10-year period from 1969 to 1978 and provides good time resolution with nearly biweekly sampling. The data were well distributed seasonally, with 16 to 23 profiles for each month of the year.

Hydrographic data from station H-3 are subject to short-period disturbances associated with internal waves in Monterey canyon (Broenkow and McKain 1972). Errors in the observations of temperature and salinity, local eddies, or other local environmental phenomena probably also contribute short-term noise in the data. However, the frequency of sampling to at least 500 m at station H-3 over a multiyear period is unique along the central California coast, and—for ocean monitoring purposes—overrides deficiencies in the data caused by high-frequency noise.

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[1] Hopkins Marine Station. CalCOFI Hydrographic Data, Collected on approximately biweekly cruises on Monterey Bay, California. Annual Reports for years 1968 to 1973 (mimeo.) Hopkins Marine Station, Pacific Grove, California 93950

[2] CalCOFI hydrographic data reports, Monterey Bay, July 1974-June 1978. Tech. Publications 75-1, 76-1, 77-1, 78-1, and 79-1. Moss Landing Marine Lab., Moss Landing, California 95039

Three distinct seasonal phases of Monterey Bay hydrography were proposed by Skogsberg (1936) and amplified by Bolin and Abbott (1963). These are the upwelling period of summer, a calm warm "oceanic" period in fall, and the Davidson Current period in winter. In January and February, surface water has a high temperature and low salinity (roughly 13°C and 33.2°/oo). As upwelling begins in spring, deep water rises, and the surface water cools and becomes more saline, reaching typical values of 9°C and 34.0°/oo in summer. Warming occurs in the oceanic period in fall, and the surface salinity decreases in winter. At depth (200 to 400 m), conditions are more stable, and the annual temperature-salinity excursions are reduced from their surface values.

The average seasonal pattern of varying oceanographic conditions in Monterey Bay is strongly modified in certain winters by changes in the vertical thermal structure (Figure 2). The 8° and 10°C isotherms were as much as 100 m deeper than their mean depths in winters of 1969-70 and 1972-73, and 20-50 m deeper in the winters 1976-77 and 1977-78. The average depth of the 8°C isotherm lies at depths of 250 and 300 m from August to January, but the 8°C isotherm was at depths of 300-420 m from August to at least November 1969 (deep data in early 1970 are missing) and from July 1972 to February 1973. The 10° and 12°C isotherms were 50-70 m deeper than normal in these two winters, but the anomalous deepenings of these isotherms did not start until October, two months later than that of the 8°C isotherm. The three isotherms were also deeper than normal in the winters of 1976-77 and 1977-78, although not as markedly so as in 1969-70 and 1972-73. Again in these winters, anomalous deepening of the 10° and 12°C isotherms lagged that of the 8°C isotherm. In almost every case, all three isotherms returned to normal depths nearly simultaneously in April or May. Isotherm depths were near normal in the winters of 1970-71, 1971-72, and 1974-75, and were consistently shallower than normal in the winter of 1975-76.

The anomalous deepenings of the deep isotherms may have occurred in two waves, with an initial depression in summer and a second depression the following winter. Anomalous depressions of isotherms were observed in summer 1969 and 1972. Although deep data in the following winters are sparse, second waves of isotherm depression the following winters appear to have occurred. Double depressions were observed in 1976-77 and 1977-78 but were of lesser magnitude than those in 1969-70 and 1972-73.

The anomalous depressions of isotherms were associated with above-normal surface temperatures in late winter. The surface water remained above 12°C until February to April during the winters when the

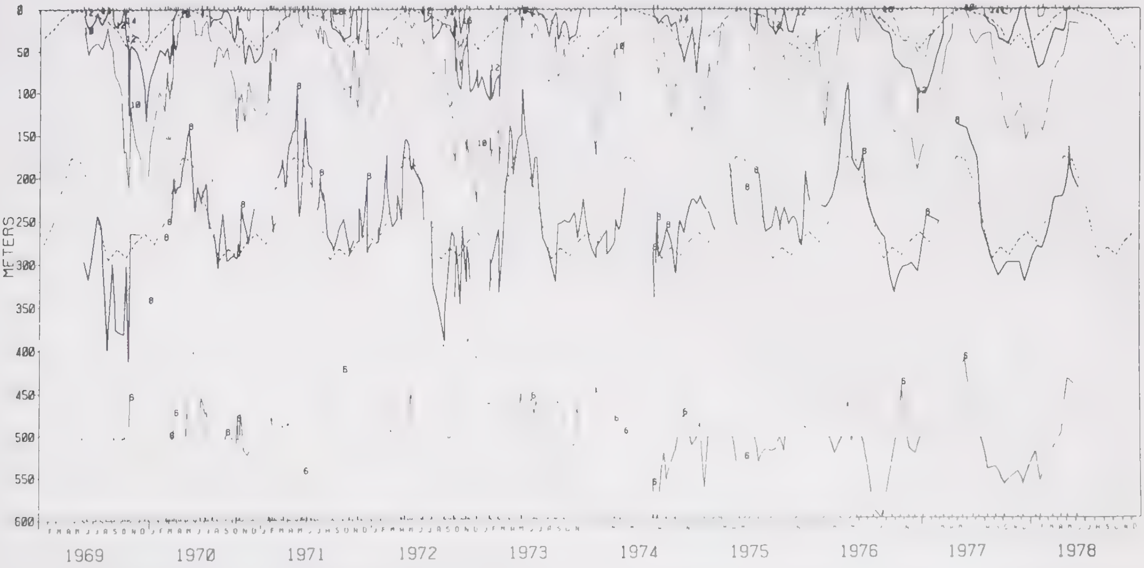

Figure 2. Time series vertical section of temperature (degrees Celsius) at station H-3. Dotted lines show long-term monthly means of 8°, 12°, and 16°C isotherms Small, inverted "T" marks show greatest depth of data at each hydrographic cast

8°C isotherm was anomalously deep, but when the 8°C isotherm was near or shallower than normal, the surface water cooled to below 12°C by October or November. (A slight exception to this was in the winter of 1977-78, when the surface water was below 12°C for a short period in November and December 1977 but then again warmed and remained above 12°C until April 1978.)

Salinity at station H-3 (Figure 3) has generally similar interannual variations. Depressions of the 34°/oo isohaline by 200 m or more occurred in late 1969 and in winter 1972-73. Lesser deepenings of 50-100 m occurred in the winters of 1976-77 and 1977-78. The 34°/oo isohaline was at near-normal depths in the winters of 1970-71, 1974-75, and 1975-76, and shallower than normal in winter 1973-74.

Wooster and Jones (1970) described the California Undercurrent as a poleward flow along the coasts of California and Baja California and recognizable by a coastward deepening of isopycnals and poleward transport of warm, saline water. They suggest that the undercurrent can be recognized by the presence of water of greater than about 34.0°/oo on the 150 cl/ton (sigma-t = 26.54) surface. To look for undercurrent water off Monterey, we plotted salinity on constant density surfaces (Figure 4). On the 26.50 sigma-t surface, there were no large increases in salinity during the period of record, and thus pulses of equatorial water were not observed off Monterey. (Isolated anomalously high temperature values of near 10°C occurred in the hydrographic cast data at 300-400-m depths in December 1969 and December 1972. These values are interesting because they occurred at times when unusually high temperatures might have been observed, but they were deleted as erroneous because XBT data from the same months and depths did not show similar high values.)

Low surface salinities were observed at station H-3 in early 1970 and early 1978 (Figure 4), probably as a result of onshore Ekman transport of low salinity offshore water. Chelton (1981) described the low salinities observed on the CalCOFI survey during winter 1977-78 and showed that the low salinity could not have resulted from precipitation alone. Reid et al. (1958) showed a core of low-salinity water (less than 33.0°/oo) on the surface 200-400 km off central California. Saur (1980) showed that, based on surface salinity observations made by ships of opportunity between San Francisco and Honolulu during 1966-74, a core of low-salinity surface water occurs off San Francisco throughout the year and tends to move onshore in spring and offshore in autumn. Onshore transport in winter (Figure 8) could force this low-salinity surface water onto the coast and could have caused the salinity minima observed at station H-3 in February 1970 and March-April 1978. Saur's data on surface salinity also agree well with station H-3 data for 1969-72. Bolin and Abbott (1963) show similar surface salinity minima in Monterey Bay in January 1956 and March 1958, following similar periods of strong onshore transport (Figure 8), although they suggest that the low salinities are primarily due to precipitation. Broenkow and

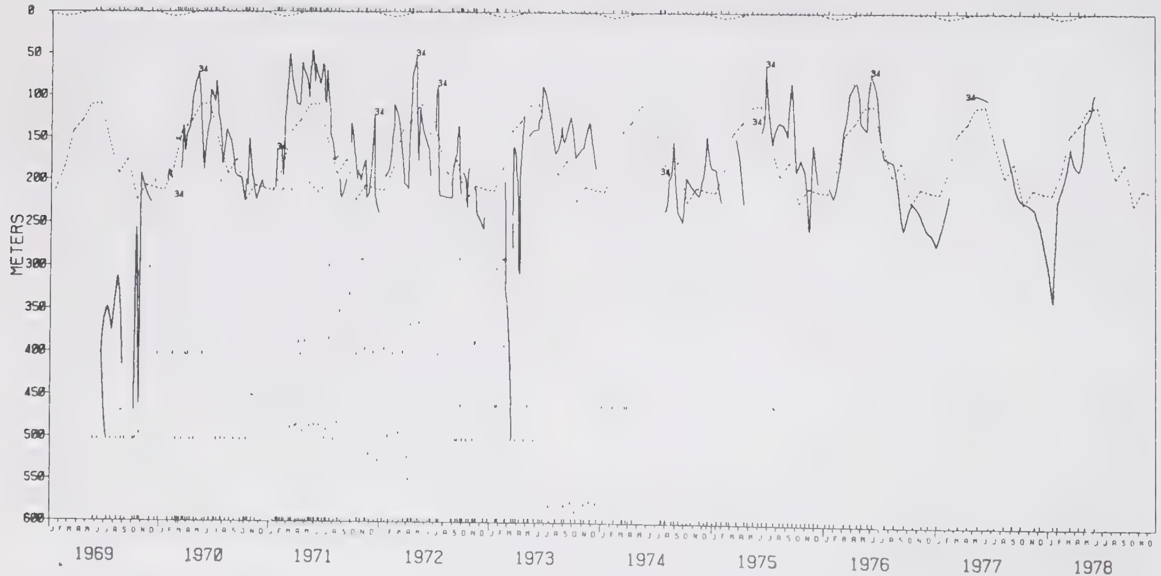

Figure 3. Time series vertical section of salinity (parts per thousand) at station H-3. Dotted lines show long-term monthly means of depth of 33 and 34.00‰ isohaline

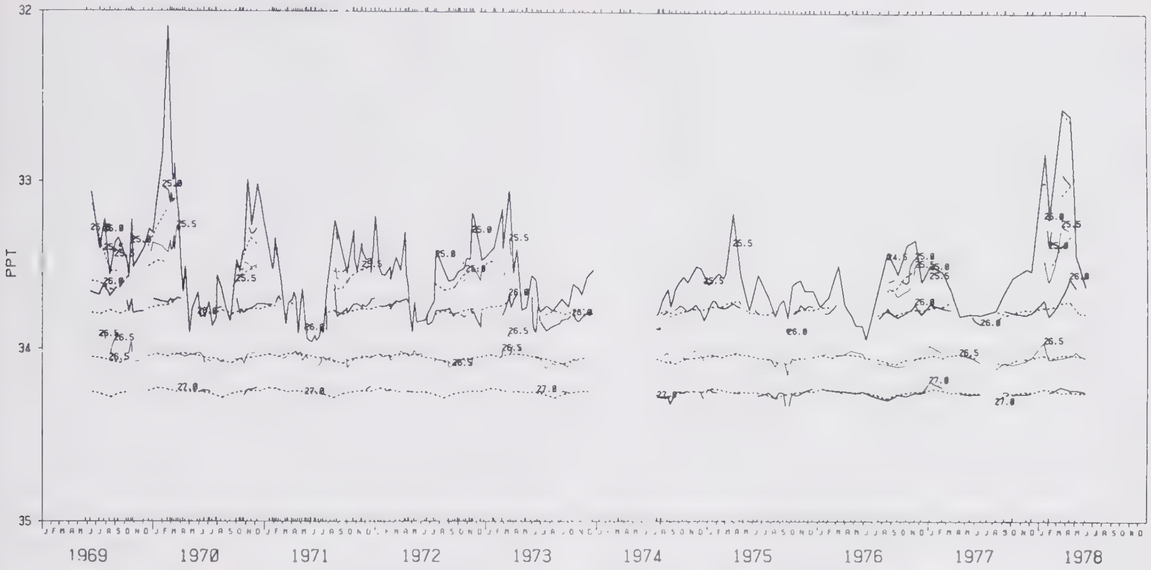

Figure 4. Time series of salinity (parts per thousand) on sigma-t surfaces at station H-3. Dotted lines show long-term monthly means.

Smethie (1978) suggest that lower salinities observed in Monterey Bay in the winter of 1972-73 relative to the winter of 1971-72 were due to more persistent southerly winds in 1972-73 and that the low salinities were associated with storms and consequent heavy rainfall and land runoff.

Dynamic height anomalies were computed for each of the hydrographic profiles at station H-3 and plotted as time series (Figure 5). Although the hydrographic casts generally extended to 500 m or more, we chose 400 m as the reference depth to allow use of the XBT observations. The mean seasonal cycle of 0/400-db dynamic height (shown as dotted lines in Figure 5) had a minimum in May or June and double maxima in

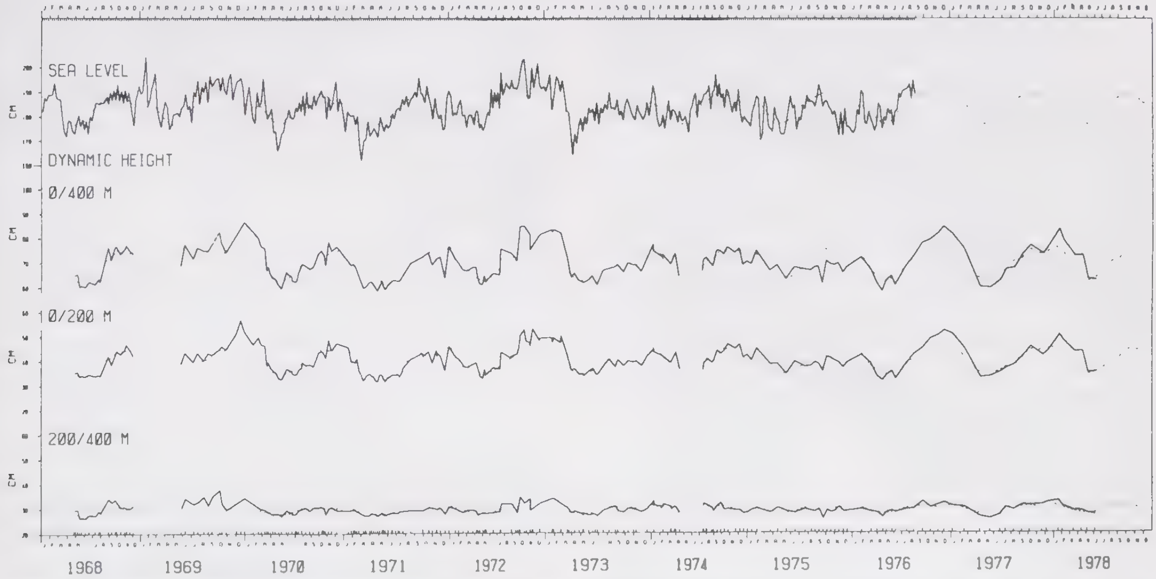

Figure 5 Time series of unadjusted weekly mean sea level (cm) at Monterey, California, and 0/400-db, 0/200-db, and 200/400-db dynamic height (dyn cm) at station H-3. Dotted lines show long-term monthly means.

September and December. The two maxima of the mean seasonal cycle of dynamic height in fall and winter are caused by the double wave of isotherm depressions mentioned previously. Because of the relative greater effect of temperature than salinity in determining density in this region, depression of the thermal structure (and consequent increased dynamic height) overrides the effect of depression of the salinity structure (in reducing dynamic height). Large year-to-year fluctuations occurred in the record of 0/400-db dynamic height with above-normal values of dynamic height in the winters of 1969-70, 1972-73, and to a lesser extent in the winters of 1976-77 and 1977-78. Below-normal values of dynamic height occurred in the winters of 1973-74 and 1975-76.

Most of the fluctuations of the 0/400-db dynamic height were caused by changes in the upper 200 m of water, as is seen by comparing time series of two components of the 0/400-db height; 0/200-db and 200/400-db heights. The 0/200-db dynamic height has a seasonal cycle that is similar to that of the 0/400-db dynamic height with double maxima, in September and December, and a minimum in April. The 0/200-db dynamic height had deviations from its mean seasonal cycle that were similar to the 0/400-db dynamic height deviations: the maxima of the 0/400-db dynamic height in the winters of 1969-70, 1972-73, 1976-77, and 1977-78 are also seen in the 0/200-db series. In contrast to the fairly regular seasonal cycle of the 0/200-db series, the 200/400-db series of dynamic height has little seasonal variation and has minor maxima in the winters of 1969-70 and 1972-73 and a minimum in summer 1977. The maxima in the winters 1969-70 and 1972-73 are associated with the depressions of the thermal structure to depths below 200 m.

Sea level at Monterey had interannual fluctuations similar to the 0/400-db dynamic height (Figure 5). The data plotted are weekly means of hourly sea-level elevations at the Monterey tide gage and were not adjusted for atmospheric pressure fluctuations. The sea-level data show high-frequency fluctuations of 10-20-day period that may be due to pressure changes. Fluctuations of longer period appear to be correlated well between the two series.

The interannual fluctuations of dynamic height at station H-3 and sea level at Monterey are apparently due to large-scale, coast-wide variations in the alongshore currents. If the anomalous depressions of isotherms and related anomalous increases of dynamic height occur primarily near shore, and conditions offshore are more stable from year to year, the anomalous thermal conditions would cause anomalous increases in the slope of the sea surface toward the coast and, hence, anomalous increases in poleward alongshore currents. Thus the time series of dynamic height and related sea-level variations can provide an index of the interannual changes in the flow of the California Countercurrent. Not only can the series of dynamic heights show interyear differences of poleward transport, but on a finer time scale the series may even indicate shorter period changes. The apparent correspondence between dynamic height and sea-level changes on monthly time scales may confirm this.

No long time series of observations of transport of the countercurrent are available for direct comparison with the dynamic height index. The only data on alongshore currents available are from hydrographic surveys, current meters, ships of opportunity, and drifter studies. Many of these data are of short duration and are scattered in time and thus cannot be easily used to resolve interyear differences. We shall examine each of the data sources for comparison with the hypothesized fluctuations of the countercurrent flow, based on the time series of 0-400-db dynamic height from station H-3.

RATIONALE FOR COUNTERCURRENT INDEX

A rationale for a relation between interannual fluctuations of dynamic height at station H-3 and strength of the California Countercurrent can be made based on the data collected on the CalCOFI hydrographic surveys that have been conducted along the coasts of California and Baja California since the early 1950s. Published charts of 0/500-db and 200/500-db dynamic height for particular CalCOFI surveys show that during periods of higher than normal dynamic height at station H-3, intensified poleward flow occurred along the coast.

Direct comparison of time series of CalCOFI and station H-3 data are not possible because the CalCOFI survey data are available much less frequently than station H-3 data. The CalCOFI surveys were not made at regular time intervals but instead were made nearly monthly in some years, quarterly in other years, and not at all in still other years. We compared annual means and seasonal cycles of dynamic height from the two sources. We recognize that different individual years are included in each set of monthly means but neglect the errors introduced. The data for CalCOFI lines 67 and 70 off central California for years 1958-78 were obtained.[3] The data on annual means of dynamic height at station H-3 are based on at least 12 hydrographic casts per month, but annual means of the CalCOFI data are limited by inadequate sampling in certain months, as pointed out by Chelton (1980). For example, there were several months in which no observations were available and several others when only one observation was made.

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[3] L. Eber, Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, CA 92037

The annual and seasonal ranges of the monthly means are shown in Figure 6. The annual mean dynamic heights on line 70 off Point Sur, south of Monterey, show that the dynamic height normally slopes downward from the coast to a trough 30-40 km offshore (near station 55) and then rises in an offshore direction. By geostrophy, the downward slope from the coast is associated with northward alongshore flow, and the upward slope offshore beyond the trough is associated with southward flow. Chelton (1980) has fit the annual variations of CalCOFI survey data with two harmonics and plotted monthly maps of dynamic height along the California coast. Chelton's maps show a trough off Monterey, parallel to the coast from September to February and located 100-200 km offshore.

The magnitude of the range of annual variations of dynamic height is greatest at the coast and decays in an offshore direction (Figure 6). Since station H-3 is well inshore of the trough and since inshore variability is greater than that in the trough, fluctuations of dynamic height at station H-3 reflect fluctuations of the slope of dynamic height normal to the coast and hence variations of the countercurrent. Huyer (1977) found that off Newport, Oregon, there was a minimum of seasonal variation of steric height about 80 km from the coast.

The trough of dynamic height weakens and moves inshore in summer. This can be seen in monthly distributions of 0/500-db dynamic heights along lines 67, off Monterey Bay, and 70, off Point Sur (Table 1). Nearshore observations are not available from these lines, and thus data from station H-3 are assumed to represent inshore variations along the lines. Mean dynamic height is computed for each station and month, even if only a single observation was available for that location. The number of observations ranges from 1 to 15, with generally greater sampling on line 70 than line 67. (There were 131 observations on line 67, and 211 on line 70.) On lines 67 and 70, the trough of dynamic height (indicated in Table 1 by dynamic heights of less than 80 cm) is generally located near stations 53 or 55 but moves inshore and disappears in June or July. In summer, because of northwesterly winds, alongshore surface wind stress off Monterey is large, with peak values in May or June (Nelson 1977). Wind stress causes upwelling along the coast, and the thermal structure slopes upward toward the coast. The nearshore surface current becomes southerly, weakening the countercurrent and causing the California Current to move inshore and override the countercurrent. These processes cause a redistribution of mass so that the trough of dynamic height moves inshore and disappears in summer.

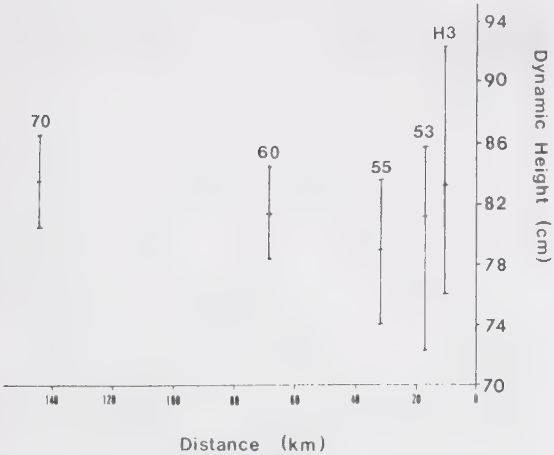


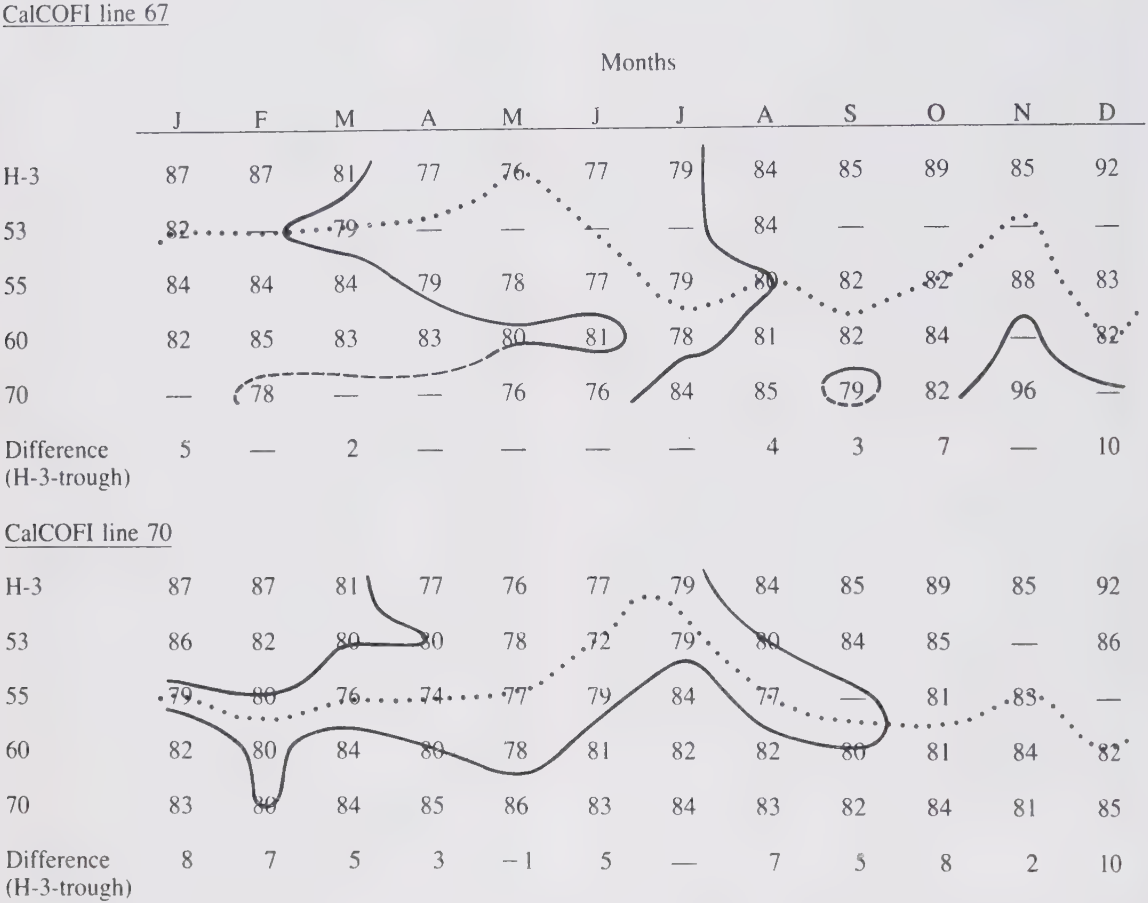
Figure 6. Annual means and seasonal ranges of 0/500-db dynamic height (dyn cm) at station H-3 and along CalCOFI line 70

An index of countercurrent transport can be made by calculating the difference of dynamic height at station H-3 and the trough minimum. This difference (Table 1) is greatest from October to February, with peak values in December, suggesting that maximum countercurrent flow occurs in December. This is in agreement with plots of Hickey (1979), which show strongest northward alongshore flow from November to January.

COMPARISON WITH TIME SERIES SEA-LEVEL DATA

Reid and Mantyla (1976) have shown that in the North Pacific south of about 40°N, monthly mean sea levels are typically highest in late summer and early fall and lowest in winter as a consequence of the annual heating and cooling cycle. North of about 40°N, however, the seasonal cycle shifts phase, and sea levels are highest in winter and lowest in summer. This phase shift cannot be explained by seasonal heating and cooling. Reid and Mantyla showed that the high sea levels of winter are instead a consequence of the circulation of the subarctic cyclonic gyre of the North Pacific Ocean. The California Countercurrent can be considered a southern arm of the cyclonic gyre along the California coast. The countercurrent has strongest flows in winter, causing sea level to slope upward toward the coast and accounting for the phase shift south of 40°N. Sturges (1974) accounted for high sea levels and dynamic heights near Neah Bay, Washington, in terms of stronger northward along-

TABLE 1
Monthly Mean 0/500-db Dynamic Height (cm) at Station H-3 and at Stations on CalCOFI Lines 67, off Monterey Bay, and 70, off Point Sur



CalCOFI line 67

	Months											
	J	F	M	A	M	J	J	A	S	O	N	D
H-3	87	87	81	77	76	77	79	84	85	89	85	92
53	82	—	79	—	—	—	—	84	—	—	—	—
55	84	84	84	79	78	77	79	80	82	82	88	83
60	82	85	83	83	80	81	78	81	82	84	—	82
70	—	78	—	—	76	76	84	85	79	82	96	—
Difference (H-3-trough)	5	—	2	—	—	—	—	4	3	7	—	10

CalCOFI line 70

	J	F	M	A	M	J	J	A	S	O	N	D
H-3	87	87	81	77	76	77	79	84	85	89	85	92
53	86	82	80	80	78	72	79	80	84	85	—	86
55	79	80	76	74	77	79	84	77	—	81	83	—
60	82	80	84	80	78	81	82	82	80	81	84	82
70	83	80	84	85	86	83	84	83	82	84	81	85
Difference (H-3-trough)	8	7	5	3	−1	5	—	7	5	8	2	10

Tables are contoured, and dotted line indicates trough of dynamic height. Difference of monthly mean dynamic height at H-3 and trough is also shown

shore currents in winter. Similarly, Marthaler (1976) compared monthly mean sea level at Newport, Oregon, with currents observed with current meters on the continental shelf off Newport during 43 different months. He found that sea level and alongshore currents were strongly correlated, with best correlations from November to May or June when northward flows were strongest.

Sea level at Monterey is closely correlated with dynamic height at station H-3 for the years of common record (Figure 5; Bretschneider and McLain 1983). Sea level at other stations along the West Coast from Los Angeles to Neah Bay, Washington, (Figure 7) had similar year-to-year variability in the dynamic height at station H-3. Periods of above-normal sea level generally occurred in the latter portions of certain years: 1951, 1957, 1958, 1963, 1965, 1969, 1972, 1976, and 1977. Below-normal sea levels occurred in 1948, 1949, 1955, 1956, 1973, and 1975. Because of the similarity of sea level and dynamic height in years when both data series are available, sea level can also be used as an index of alongshore currents off central California (Chelton 1981). This relation allows inexpensive monitoring of alongshore currents from shore stations on an interannual time scale rather than by expensive ship surveys.

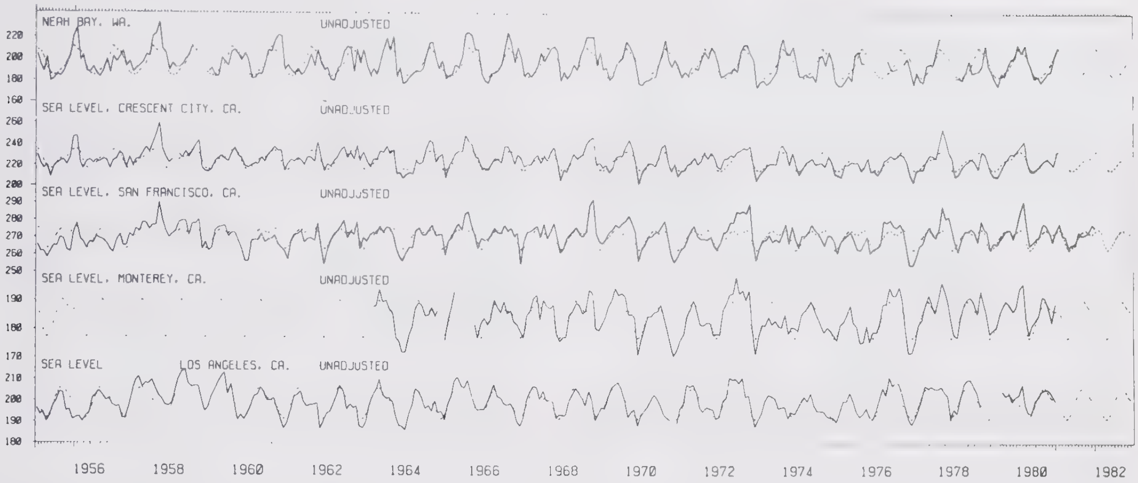


Figure 7. Time series of sea level (cm) at selected West Coast tide gage stations. Data have not been adjusted for atmospheric pressure effects. Dotted lines show long-term monthly means.

COMPARISON WITH SHIPS-OF-OPPORTUNITY XBT DATA

Approximately biweekly sections of sea-surface temperature, salinity, and subsurface temperature have been made since 1966 by expendable bathythermograph (XBT) from ships of opportunity on the route from San Francisco to Honolulu (Saur et al. 1979). The XBT drops were made at approximately 120-km intervals along the route, with sections repeated at approximately 2-week intervals. Price (1981) has computed dynamic heights from these XBT data and has computed an index of strength of the countercurrent. Price used climatological hydrographic data to compute long-term mean temperature-salinity relationships and thus to estimate salinity from observed temperature data. This method of monitoring ocean currents has the advantages of relatively low cost (compared to repeated hydrographic observations from research vessels) and good time resolution but suffers from limited depth range and possible inaccuracies in the estimation of salinity. The XBT drop closest to the coast was often 100 km or more offshore, and thus the observations may have often missed the countercurrent. In spite of the problems, Price's index of the flow of the countercurrent (called V4) shows fair agreement with estimates of countercurrent flow from station H-3 dynamic height data and with sea-level data at both Monterey and San Francisco. All series show high values in late 1969 and in late 1972-early 1973, and low values in 1968, 1970, late 1973, and 1974. Price's index shows a very strong double peak in 1972-73; this may be related to the double waves of isotherm depression seen at station H-3.

COMPARISON WITH HYDROGRAPHIC AND DRIFTER DATA

The available hydrographic and sea-level data indicate significant interannual fluctuations of alongshore currents. The periods of strong flow are discussed below and compared to available hydrographic survey and surface drifter observations.

1957-59

High sea levels (Figure 7) were observed from 1957-59, suggesting a period of anomalously strong northward alongshore currents. Reports presented at the Rancho Santa Fe Symposium in 1958 described numerous unusual oceanographic and biological events observed in 1957 and 1958; these were attributed to anomalous northward coastal flow. Schwartzlose (1963) noted very strong northward transport of drift bottles along the coast in 1958. Tully et al. (1960) described anomalous increases in water temperature off British Columbia in 1957 and 1958.

1969-70

The computed dynamic height values from station H-3 were above normal in July and August 1969, peaked in December, and declined to relatively low values by May 1970. Schwartzlose and Reid (1972) considered that the Davidson Current was well developed in November 1969. Drift bottle recoveries indicated that coastal water was flowing northward from southern California at a minimum speed of 13 km/day. Recovery records for CalCOFI drift bottle studies (Crowe and Schwartzlose 1972) showed considerable northward flow in both October and November 1969 from central California. Several drifters released off central California during these months were recovered in southeastern Alaska, and numerous recoveries came from Oregon and Washington. The magnitude of northerly flow noted during these months was comparable to that observed during November 1957 and January 1958.

1972-73

Wickham (1975) made hydrographic and drogue surveys off Monterey in early August of 1972 and 1973. His data show that water between the surface and 500 m was warmer, more saline, and had a greater northward velocity during August 1972 than August 1973. Water in August 1972 appeared to have "southern" characteristics similar to water observed by Molnar (1972) inshore of a transition zone south of Point Arguello during June 1972. Water offshore of this transition zone had "northern" characteristics similar to water found off Monterey in June. Wickham (1975) further suggested that water observed near Monterey in August 1972 was southern water advected northward from the region of Point Arguello at a speed of at least 5 cm/sec. This is in agreement with the station H-3 data, which show that an intrusion of relatively warm water into Monterey Bay began sometime in June or July 1972 (Figures 3 and 5).

Additional evidence of intensification of the countercurrent in June-July 1972 appears in the hydrographic and current studies of Broenkow and Smethie (1978). Based on hydrographic data from station H-3 between 1971 and 1973, they concluded that local upwelling events, evidenced by a shallowing of near-surface isotherms, generally corresponded to peaks in local northerly winds. They noted an exception to this relationship in July 1972, however, when a temperature maximum occurred despite the presence of northerly winds.

In a surface study, Blaskovich (1973) released drift cards monthly in Monterey Bay between September 1971 and April 1973. He found southward flow from March to May1972, but from June to September 1972 most recoveries were made on the eastern shore of Monterey Bay, indicating a lack of typical summer southward flow. In another drifter study conducted in the Monterey Bay area between November 1971 and April 1973, Griggs (1974) found a good correlation between southward surface drift and northerly winds from March to May 1972. The relationship broke down in June, July, and September 1972, when drifter recoveries demonstrated substantial northward surface flow despite the presence of northerly winds.

Evidence that the intensification of the countercurrent in 1972 was not confined to central California waters can be found in the results of a drift-bottle study conducted from early March to early August 1972 off northern Oregon (Rothlisberg 1975). Northward surface drift persisted from March to mid-April. Currents in late April were transitional, with a large southerly component, and recoveries in May indicate that southward flow had become dominant. In spite of strong northerly winds from May through August, however, a reversal to northward flow was indicated by recoveries from June and July releases.

Broenkow and Smethie (1978) concluded from the station H-3 hydrographic data that northward flow in the winter of 1972-73 was stronger than that of the previous winter. This result was also shown by drifter releases during the winters of 1971-72 and 1972-73, which indicated northward flow in both winters but long-distance drifts only during winter 1972-73. Blaskovich (1973) reported the recovery of a drift card in Oregon that was released in October 1972 at Monterey, as well as an Oregon recovery and a Washington recovery from November 1972 releases. Paradoxically, another card released in October 1972 found its way south to San Simeon, a distance of 150 km. Griggs (1974) does not give detailed accounts of individual drifter movements, but recoveries during December 1972 and February 1973 indicated that a more extensive northward flow occurred during this period than from November 1971 to February 1972. Griggs, like Blaskovich, found both long-distance southern and northern movement during October 1972.

1976-77

Anomalously high dynamic heights at station H-3 in 1976-77 would indicate that intensification of northward alongshore flow may have started in June 1976 and reached its maximum influence by the end of December. Comparative data are unavailable off central California, but Tsuchiya (1980) summarized the results of nine nearshore cruises off southern California from 1974-77. Tsuchiya found that during October 1976 to January 1977, the water in the upper 300 m was warmer and more saline than normal. He related the change to a large-scale warming of the eastern North Pacific, but an intensification of northward flow along the coast at the time may also have been a cause.

A decline of dynamic height values to lower than normal occurred in summer 1977, suggesting a period of stronger than normal southward flow. The dynamic height data indicate that an intensification of the countercurrent began in fall 1977 and apparently peaked in

January 1978 (one month later than in the previous winter) before declining to minimum values in May 1978. A cooperative United States-Poland oceanographic survey was conducted along the west coast of the United States during August and September 1977 (Ingraham and Love 1978). Geostrophic currents derived from the survey data indicate that surface flow was generally southward all along the coast, but flow at 150 m (computed relative to 500 db) was generally northward except in the vicinity of the Columbia River. Ingraham and Love considered these observations to be evidence that a substantial northward flow existed at depth during late summer 1977 over the outer continental shelf and slope. Gardner (1982) found evidence of Pacific equatorial water on the continental shelf north of Vancouver Island in April and November 1977, with greater amounts in November.

CAUSES OF COUNTERCURRENT FLUCTUATIONS

Several processes act in concert to drive alongshore currents. Hickey (1979) has described the countercurrent in terms of wind stress and the curl of the wind stress. Wind stress seems the more important. Several studies off Oregon (e.g., Cutchin and Smith 1973; Huyer et al. 1978) have shown that currents over the continental shelf observed with moored current meters are highly correlated with sea level at nearby tide gages and that both respond rapidly to changes in forcing by alongshore winds.

Sharp drops of both dynamic height at station H-3 and sea level at Monterey occurred in early 1970, 1973, and other years. This suggests that the transition between northward and southward flow in spring may be rapid. Huyer et al. (1979) describe sharp flow reversals off Oregon during March of both 1973 and 1975. They refer to these current reversals as a "spring transition" and suggest that such reversals occur each spring and represent a relatively permanent change from winter (northward flow) to summer (southward flow) conditions on the shelf. The time series of dynamic height at station H-3 (Figure 5) suggests that such pronounced reversals do not occur every year and may be weak or oscillatory, as in 1971, 1974, and 1975. Spring reversals following winters of above (below)-normal sea level and dynamic height tend to be more (less) intense than normal.

Whereas the mean seasonal cycle of dynamic height at station H-3 suggests that southward flow occurs during the first half of the year and northward flow during the second half of the year, reversals of the direction of flow are common within both periods. These can be seen as sharp reversals of dynamic height at station H-3 and can be explained by assuming that on large space scales, water to the north of H-3 is colder than that to the south. Northward flow (or anomalously weak southward flow) would then cause increased water temperature (averaged over the upper 400 m) and consequently, increased dynamic height (assuming also that salinity effects are small). Conversely, southward flow (or anomalously weak northward flow) would cause decreased water temperatures and dynamic heights. Thus reversals of the time slope of dynamic height at coastal locations such as station H-3 can reflect reversals of coastal flow.

Evidence that fluctuations in the dynamic height reasonably depict actual current reversals is available from drifter movements in 1972. The dynamic height data suggest that a sharp reversal in currents occurred between mid-September and mid-November 1972. The implied strong northward flow followed by strong southward flow is substantiated by the long-distance transport of drifters, both to the north and south, reported to have occurred in October 1972 by Blaskovitch (1973) and Greggs (1974).

Sverdrup transport set up by curl of the wind stress over the region is a second process driving the countercurrent but is less well understood than wind stress itself. Nelson (1977) has computed and plotted monthly maps of wind stress curl off the West Coast based on historical ships' wind observations. Nelson's maps show fine seasonal detail (about 110-km resolution) but because of scarcity of historical data, they do not show interyear variations. Chelton (1980) computed similar maps of wind stress curl, based on analyzed fields of surface pressure, which can be computed monthly but have lower spatial resolution (about 300-km resolution) than Nelson's maps and are subject to poor resolution of surface pressure gradients along coasts because of coastal mountains (Bakun 1973). Both Nelson's and Chelton's maps show general negative wind stress curl offshore and a band of positive curl along the coast, a situation that would produce poleward alongshore currents.

Nelson's maps show several peaks of positive wind stress curl along the coast: 42°N south of Cape Blanco, 38°N near Point Reyes, 34°N south of Point Conception, 31°N off northern Baja California, and 27°N south of Punta Eugenia. Chelton's maps show only one of these areas—the major feature south of Point Conception. To examine the effect of Sverdrup transport on alongshore currents, we computed time series of monthly wind stress curl at these locations along the coast for the years 1946-80 from monthly mean surface pressure fields developed by FNOC and using methods of Bakun (1973, 1975). The time series of wind stress curl did not appear to be correlated with the dynamic height series and hypothesized alongshore currents. This result is similar to that of Hickey (1979), who found little correlation of alongshore currents with wind stress curl, and with Bretschneider and McLain (1983) who found no correlation of Sverdrup transport with dynamic height at station H-3. Wind stress curl may, however, contribute a long-term net tendency for poleward alongshore currents because of the long time periods required for spin-up of a curl-driven current (Chelton 1982).

In addition to wind stress and wind stress curl, a third process that drives alongshore currents is local forcing by the component of Ekman transport toward the coast and resultant depression of the isotherms near the coast. Cairns and Lafond (1966) described short-period fluctuations in shallow water off San Diego, caused by onshore Ekman transport. The process seems of greater importance on longer time and space scales. Southerly winds and resulting onshore transport are relatively infrequent off California but become increasingly common in winter with distance to the north so that onshore transport and downwelling occur each winter along the coasts of the Pacific Northwest and the Gulf of Alaska (Bakun 1973). Figure 8 shows the time series of the component of Ekman transport normal to the coast, again computed by the methods of Bakun. Off California at latitudes 36°N and 39°N, there were anomalously strong onshore Ekman transports during the winters of 1957-58, 1960-61, 1969-70, 1972-73, 1977-78, and 1979-80. Anomalously strong onshore transport would cause anomalous depression of the thermal structure and consequently cause anomalously high sea level and dynamic height along the coast. Northward flow would result from upward slope of the sea surface toward the coast. Thomson (1972) proposed onshore Ekman transport as an explanation for annual variations in the northward penetration of relatively warm water off the British Columbia coast during 1955-56. Douglas and Wickett (1978) explained above-normal bottom-water temperatures on the continental shelf off Vancouver Island in February-March 1978 as a result of anomalously strong onshore Ekman transport.

A fourth process that drives alongshore currents on interannual time scales is remote forcing by propagation of a depression of the thermocline polewards along the coast from the Eastern Tropical Pacific. McCreary (1976) and Hurlburt et al. (1976) modelled the effect of a weakening of the trade winds over the equatorial Pacific and a resultant depression of the thermocline along the coast of Peru. They showed that the depression would be propagated both to the north and south along the coast as a coastally trapped Kelvin wave. Associated with the wave are poleward coastal jets formed by quasi-geostrophic adjustment to the depressed pycnocline along the coast. Enfield (1981) reviewed the available literature on this process, and Mysak et al. (1982) looked for effects of baroclinic waves in physical and biological time series data along the coast.

A major realization of this process occurred in 1972 when a strong El Niño occurred off Peru, and warm water intruded into the area and depressed the thermocline. Wyrtki (1975) presented monthly maps of the topography of the 15°C isotherm surface off Peru, and Enfield (1981) presented temperature sections off Ecuador and Peru during the event. Their data show

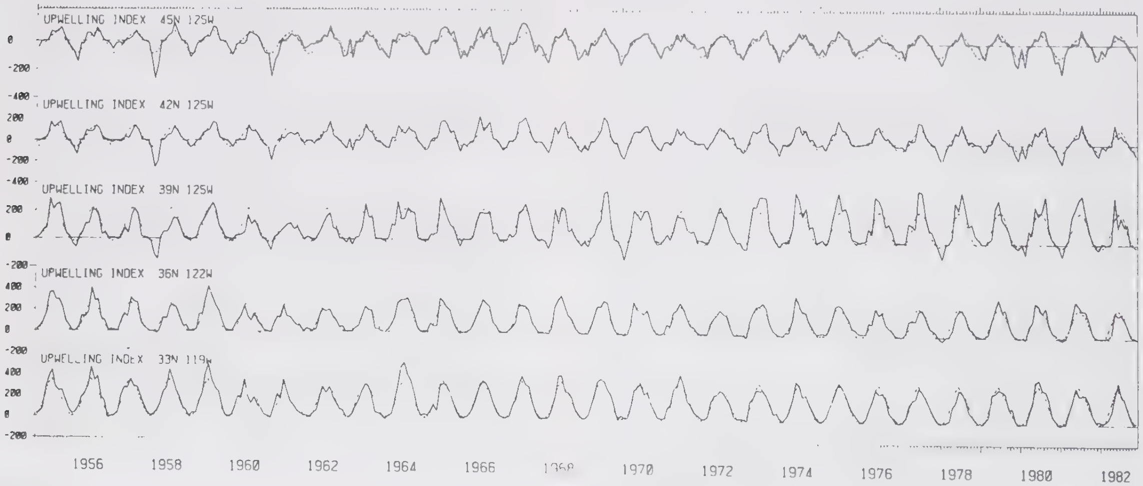


Figure 8. Time series of component of Ekman transport normal to the coast (m^3/sec/100 m of coastline) at selected locations along the West Coast. Data computed by methods of Bakun (1973, 1975). Dotted lines show long-term monthly means

that the 15°C isotherm is often within 20 m of the surface, or surfaces off the Peruvian coast with coastal temperatures less than 15°C. During the 1972 event, however, the 15°C isotherm was depressed along the coast to depths of 20-100 m in February-March, 60-120 m in August-September, and 150-250 m by December.

The anomalous depression of the thermal structure was observed to propagate both to the north and south. Wyrtki (1975) described changes observed to the south in the depth of the 26.4 sigma-t surface off northern Chile during the 1972 event. During normal years, this surface is between 50 and 100 m along the Chilean coast and deepens to 150-200 m at about 300 km offshore. During June to August 1972, the surface was depressed to depths of 200-300 m all along the coast of northern Chile. It was deepest near the coast and rose to depths of less than 150 m about 200 km offshore, implying a poleward alongshore current.

The propagation of the wave northward from the equator is poorly documented because of lack of hydrographic observations during late 1972 off North America. The waves enter the Gulf of California and dominate conditions there (Baumgartner et al. 1979). High-frequency waves (of 10-30-day period) may be trapped by the Gulf of California and not continue up the Pacific coast of Baja California (Enfield 1981). The data series off Monterey suggests that waves of lower frequency continued up the coast and caused maximum depression of the thermocline in Monterey Bay in December 1972.

The propagating wave can be seen in monthly mean sea-level data. Bretschneider and McLain (1979) showed that sea level at stations from Chile to Alaska had coherent fluctuations at low frequencies over long stretches of coast. These fluctuations were apparently associated with El Niño phenomena in the Eastern Tropical Pacific. Enfield and Allen (1980) explained the coherence by poleward-propagating coastally trapped Kelvin waves. Bretschneider and McLain (1983) presented time-distance isogram plots of anomaly of monthly mean sea level at stations along the coast from Peru to Alaska for 1963 to 1974. Their figures show that in January 1972, a period of anomalously high sea level developed off Peru and persisted throughout the year. The region of anomalously high sea level expanded northwards and reached California by July or August 1972. A second, stronger pulse reached San Francisco in October to December 1972. These waves were apparently related to the double wave of isotherm depression observed at that time at station H-3. Enfield (1981) explained the double waves of isotherm depression and associated peaks of high sea level off Peru as oceanic events related to relaxation of winds over the mid-Pacific, subsequent recovery, and on successive reflections of Kelvin and Rossby waves off the eastern and western ocean boundaries.

The four processes—wind stress, Sverdrup transport, onshore Ekman transport, and propagation of disturbances from the tropics—do not act in unison but have independent effects that may act in different combinations each year. Many of the years of high sea level and dynamic off-California height were years of El Niño events in the Eastern Tropical Pacific (e.g., 1958, 1963, 1972, and 1976) while others (e.g., 1957-58, 1960-61, 1969-70, 1972-73, 1977-78, and 1979-80) had winters of local onshore transport (Figure 8). Years such as 1973 and 1975 had normal or below-normal values of both dynamic height and sea level and were years in which neither El Niño nor anomalously strong Ekman onshore transport occurred. In 1976, there was an El Niño in the Eastern Tropical Pacific that apparently created a coastal Kelvin wave, which caused the observed depression of the isotherms at station H-3 and the hypothesized increased countercurrent flow the winter of 1976-77. In contrast, in 1977 there were normal conditions in the tropics, but strong onshore Ekman transport at 36°N in December 1977 and January 1978 apparently caused the depression of isotherms at station H-3 the winter of 1977-78. In some years, such as 1958 and 1972, both processes occurred and reinforced one another.

The characteristic time scales of these processes differ, and thus it may be possible to distinguish between them. Onshore Ekman transport is related to atmospheric fluctuations and persists only one or two months, whereas the effects of propagating coastal waves persist for several months or longer. Evidence for this is seen in 1976 when the peak of dynamic height was long-lasting and probably related to a propagating coastal wave. In 1977, when onshore transport apparently caused the anomalously high dynamic height, the peak lasted only a month or so.

The timing of the peaks of dynamic height may give clues to the processes causing them. Hickey (1979) suggested that the speed of the undercurrent has two seasonal maxima, one in summer and the second in winter, but she cannot easily relate the maxima to variations of wind stress and wind stress curl. Alternately, the double maxima of speed of the undercurrent may result from (1) the double maxima of isotherm depression in years of strong coastal wave propagation, (2) a combination of a summer peak caused by coastal propagating waves and a winter peak caused by onshore Ekman transport, or (3) some combination of these processes.

Hickey (1979) also suggested that the intensity of the summer maximum of the undercurrent increases toward the south, whereas the winter maximum decreases toward the south. She could not, however, explain these relations from distributions of wind stress and wind stress curl. These relations would be consistent with an explanation of the summer maximum related to poleward-propagating coastal waves (which originate to the south) and the winter maximum related to onshore Ekman transport (which is a local process along the coast).

EFFECTS OF THE COUNTERCURRENT ON MARINE ORGANISMS

Fluctuations in strength of the countercurrent have had notable effects on the distribution and abundance of various marine organisms. Many of these effects are poorly understood and documented, but available observations of unusual distributions of organisms do agree fairly well with the hypothesized fluctuations of the countercurrent. Only a few examples can be given here, and much research remains to be done on these effects. Radovich (1961) described many such unusual occurrences during the "warm-water" years 1957-59 and earlier, particularly in 1926, 1931, and 1941. He recognized that some of the occurrences were more closely associated with changes in the flow of the countercurrent than with increases in water temperature.

Phytoplankton

Bolin and Abbott (1963) described fluctuations of the countercurrent and associated phytoplankton catches off central California for the years 1954 to 1960, and Abbott and Albee (1967) updated the series for 1961 to 1966. Garrison (1979) provided additional data for the years 1976 and 1977. All the authors found significant year-to-year variations, with plankton organisms characteristic of low latitudes more prominent in the warm years. They suggested the importance of advection effects in causing the changes. Also, a general northward extension of subtropical and tropical phytoplankton during the warm years was noted by Balech (1960).

Zooplankton

Blackburn (1979) described fluctuations in the distribution of the salp *Doliolum denticulatum* off California during 1969. He noted that the earlier work of Berner and Reid (1961) had shown that the distribution of *Doliolum* was unusual in 1957 and 1958 in that some *Doliolum* remained inshore off southern California during the winter of 1957-58, whereas in 1949-55, they had not. Blackburn also noted that the distributions in 1969 were more similar to those in 1957-58 than to those in 1949-55. This supports the conclusion that both 1957-58 and 1969 were years with strong northward intrusions of southern water. Other species of invertebrates that have well-documented northern extensions of their range during warm-water years are the sand crab, *Emerita analoga*, (Efford 1970) and two euphausiids, *Euphausia eximia* and *Nyctiphanes simplex* (Brinton 1960).

Hubbard and Pearcy (1971) studied the distribution of salps in plankton collections off Oregon in the years 1961-64. They found that during these years several salps of probable southern origin, particularly *Thalia democratica*, occurred only in late 1963. This was a period of slightly higher than normal sea level and, although no dynamic height data are available from station H-3, probably stronger-than-normal countercurrent.

Gardner (1982) observed the occurrence of several subtropical zooplankton species in samples taken along the British Columbia coast in April and November 1977. He noted more widespread occurrence of the subtropical forms in November than April and associated their occurrence with a warm-water intrusion.

During 1978, salps were observed in large numbers off British Columbia and southeastern Alaska and were associated with other unusual observations (Lasker 1978; McLain and Ingraham 1980). As has been mentioned, onshore transport the previous winter caused intensified northward flow in 1978 and may explain these observations.

Pelagic Red Crab

Pelagic red crab, *Pleuroncodes planipes*, are normally found off the central and southern coast of Baja California (Mais 1974). The range of the species extended north as far as Monterey during the warm period from mid-1957 to early 1960 (Berner 1960; Glynn 1961; Longhurst 1967). Longhurst examined CalCOFI data from 1955-60 and distinguished two periods (1955-57 and 1958-60) with dissimilar latitudinal distributions of red crab. A northward extension of their range began in June and July 1957 in the area between Point San Eugenia and Cape Colnett, Baja California. By October 1957, crab were found near Ensenada, and in December they appeared off San Diego. In 1958 the main population probably moved no farther than San Diego, but isolated groups may have moved as far north as Monterey. In late 1958, northward movement began again, and by early 1959, crab were widely distributed north to San Pedro. Massive strandings occurred at San Pedro in 1959; by early 1960, the northward extension seemed to have ceased. Glynn (1961) reported massive strandings of red crab at Monterey in January 1960. CalCOFI data indicate that a general retreat of the northward range extension began in January 1960 (Longhurst 1967). By the end of 1961 the northern limit and center of abundance had shifted southward to about the same latitude as in mid-1957. Longhurst concluded that some factor other than temperature was responsible for this unusual northward movement. He believed that some alteration in circulation allowed crab to be swept north by coastal countercurrents.

Subsequent to the warm years (1957-60), red crab were found on Monterey beaches in the winters of 1969-70 and 1972-73 (Hardwick and Spratt 1979). The appearance of red crab north of their usual range in these winters had also been observed on Fisheries Resources Sea Surveys of the California Department of Fish and Game. The following observations were extracted from reports of those surveys.

Sea surveys to assess biomass of northern anchovy, *Engraulis mordax*, were conducted several times a year off southern California and Baja California from 1964-78. In 1979 and 1980, the number of surveys was reduced. On the surveys in November-December 1969, red crab were found consistently north of their usual range—as far north as La Jolla, California. By February 1970, crab were absent from northern Baja California and southern California waters. Because red crab were found on Monterey beaches during this period, some crabs must have moved through southern California waters undetected.

The Fisheries Resources Sea Surveys reported that large quantities of red crab were again found off Los Angeles in February 1973. "Quantities far exceeded previous observations including the warm-water years of 1957-58." Red crab maintained a presence off southern California through August 1973. By October 1973 their occurrence was unusual, a few still being found near San Diego.

Unusual observations were made in January 1977 when crab were found north to Cape Colnett, Baja California. Red crab appeared again a little farther north at Ensenada in January-February 1978. In February 1979 no unusual observations were noted, but by April 1979 the Sea Surveys reported the "most extensive influx of this species since 1973 occurred. They were taken on 10 scattered stations from San Diego to Santa Cruz Island." In February 1980, crabs were found from Point Dume southward.

In many of these studies, the organisms were not only found north of their usual range, but those on the northern edges of the range extensions were found inhabiting water cooler than where they are normally found. Because of this, theories developed to explain this extension involve northward forcing by the coastal countercurrents rather than southern populations simply expanding into favorable environmental conditions.

Sockeye Salmon

Adult sockeye salmon normally return to the Fraser River by rounding the south end of Vancouver Island via the Strait of Juan de Fuca; fewer than 20% of the run return around the north end of Vancouver Island via Queen Charlotte Sound. Royal and Tully (1961) reported that in 1958, however, the fish returned in large numbers around the north end of the island, causing reduced availability to fishermen in the Strait of Juan de Fuca. Tully et al. (1960) suggested that the northward shift was associated with anomalous oceanographic conditions during 1957 and 1958. Wickett (1977) listed peak fractions of fish returning around the north end of Vancouver Island as 35% in 1958, 24% in 1966, 25% in 1967, 34% in 1972, and 22% in 1974. Blackbourn[4] provided more recent values of 56% in 1978, 33% in 1979, 70% in 1980, and 69% in 1981. The very anomalous and persistent northward displacements of sockeye migration routes in recent years correlate roughly with onshore Ekman transport off northern California (39°N in Figure 8) the previous winter and may be related to flow of the countercurrent.

CONCLUSIONS

Fluctuations of dynamic height computed from frequent hydrographic data at station H-3 in Monterey Bay during 1969-78 agree well with sea-level data at Monterey on interannual and even monthly time scales.

A trough of dynamic height exists some 20-40 km off the coast in winter and weakens and moves inshore in summer. Interannual variations of dynamic height in the trough are of smaller magnitude than the variations at station H-3 and thus to a first approximation, fluctuations of the slope of dynamic height normal to the coast can be approximated by the fluctuations of dynamic height at the coast. Thus the interannual fluctuations of dynamic height and sea level at the coast can be used as an index of alongshore currents. By geostrophy, increased (decreased) dynamic height and sea level are associated with anomalously strong (weak or even reversed) northward flow.

The cause of the interannual variations of dynamic height and sea level appear to be due to two major processes: (1) remote forcing by poleward-propagating coastal trapped waves from the tropics that depress the thermal structure along the coast in some years by 50-100 m, and (2) local forcing by anomalous onshore Ekman transport in winter. Both processes are accompanied by coastal jets, which appear as anomalously strong alongshore currents. Interannual fluctuations of wind stress are certainly important in forcing alongshore currents, but fluctuations of wind stress curl do not appear related to interannual changes of coastal sea level nor of dynamic height at station H-3.

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[4] D. J. Blackbourn, International Pacific Salmon Fisheries Comm., P.O. Box 30, New Westminster B.C. V3L4X9 Canada

Interannual fluctuations of the countercurrent appear to affect many different organisms, including phytoplankton, zooplankton, and sockeye salmon. Many of the effects are only poorly documented and understood and thus deserve further investigation.

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Management Of California's Nearshore Fishes

Richard D. Methot, Jr.

An effective management regime must be able to balance conflicting interests and evolve with changing circumstances. Conflict over the harvest of a fishery resource occurs among commercial fishermen using different gears, recreational fishermen, and environmentalists with non-consumptive interests in the resource. The conflicts rarely occur on the seas. The arenas for confrontation are the news media, legislative lobbies, fishery councils, and courts. Jurisdictional conflicts and limitations also occur. These may be interstate, international, or between state and federal agencies.

Neither the stock nor the fishery stands still while managers attempt to resolve user conflicts and protect the health of the resource. Management measures designed to regulate yesterday's problems may be inadequate or inappropriate for regulation of tomorrow's fishery. Fishing technologies change. Additionally, stock abundance and availability typically fluctuate due to natural causes. During periods of decreasing stock levels public pressure to restrict the fishery usually increases. If the decline is actually due to natural causes then by the time new regulations come into force the stock may have started its natural recovery. In this case the regulations would appear successful but their true effect would be difficult to evaluate.

Management of a resource implies regulation. However, a fishery may be regulated without attempting comprehensive management. A regulation may be as specific as an area closure to reduce conflicts between purse-seine and gill-net fishermen. On the other hand, a comprehensive management plan may include a determination of optimum yield and a scheme to harvest that yield efficiently. The data requirements for development of a comprehensive management plan are daunting. Most management discussed here falls between simple regulations and full management plans.

Several of California's nearshore species have long histories of exploitation by commercial and recreational fishermen and of regulation by the State of California through its legislature and its Fish and Game Commission. Four of these species will be considered here: chub (Pacific) mackerel *(Scomber japonicus)*, Pacific bonito *(Sarda chiliensis)*, California halibut *(Paralichthys californicus)*, and white seabass *(Atractoscion nobilis)*. Their management histories will be described briefly. The regulatory measures enacted to preserve these resources and equitably distribute the yields will be emphasized.

Catch statistics presented here have been collected and summarized by the California Department of Fish and Game (CDFG). Commercial and partyboat (commercial passenger fishery vessel—CPFV) landings through 1969 are excellently summarized in Frey (1971). Data from 1970 through 1976 have been published annually. Data since 1976 are not yet published and data for 1980 to the present are preliminary (R. Collins, pers. comm.). Catches by independent sport fishermen have been estimated by Wine (1978, 1979a, 1979b, 1982).

Chub (Pacific) Mackerel

Chub (Pacific) mackerel are one of southern California's "wetfish" that are harvested commercially by purse seine. Although fresh and smoked chub mackerel are good to eat, these fish are not prized by sport fishermen. Additionally, a school of mackerel can be a nuisance to a CPFV trying to target on more desirable species. Chub mackerel attract effort at piers and jetties, particularly from some ethnic groups. In 1981 it was the most common species landed by private sport fishermen (Wine 1982). The total sport harvest is very small compared to the commercial harvest and only the commercial harvest is regulated. The biology and population dynamics of this species have received extensive study (e.g., Parrish and MacCall 1978).

The history of the chub (Pacific) mackerel population is characterized by a long decline and a recent recovery (Fig. 1). The commercial fishery expanded during the 1920s and peaked at 73,000 tons in 1935. Catches declined during the 1940s and, by 1958 to 1964, the average catch in California was 18,000 tons. The CDFG expressed concern to the California Assembly in 1951 but no action was taken.

During 1965 to 1970, catches declined further, to less than 3000 tons annually, and concern increased for the health of the resource. In 1968, legislation was introduced to establish a moratorium on commercial fishing, but it was not until August 1970 that a two-year moratorium was established on the commercial chub mackerel fishery. To reduce the impact on other fisheries, each load of ''wetfish'' was allowed to contain 18% by weight as incidental catch of chub mackerel. Two years later, the moratorium was extended indefinitely with provisions to allow a fishery to begin when the stock recovered. The moratorium would remain in effect until the spawning stock level was over

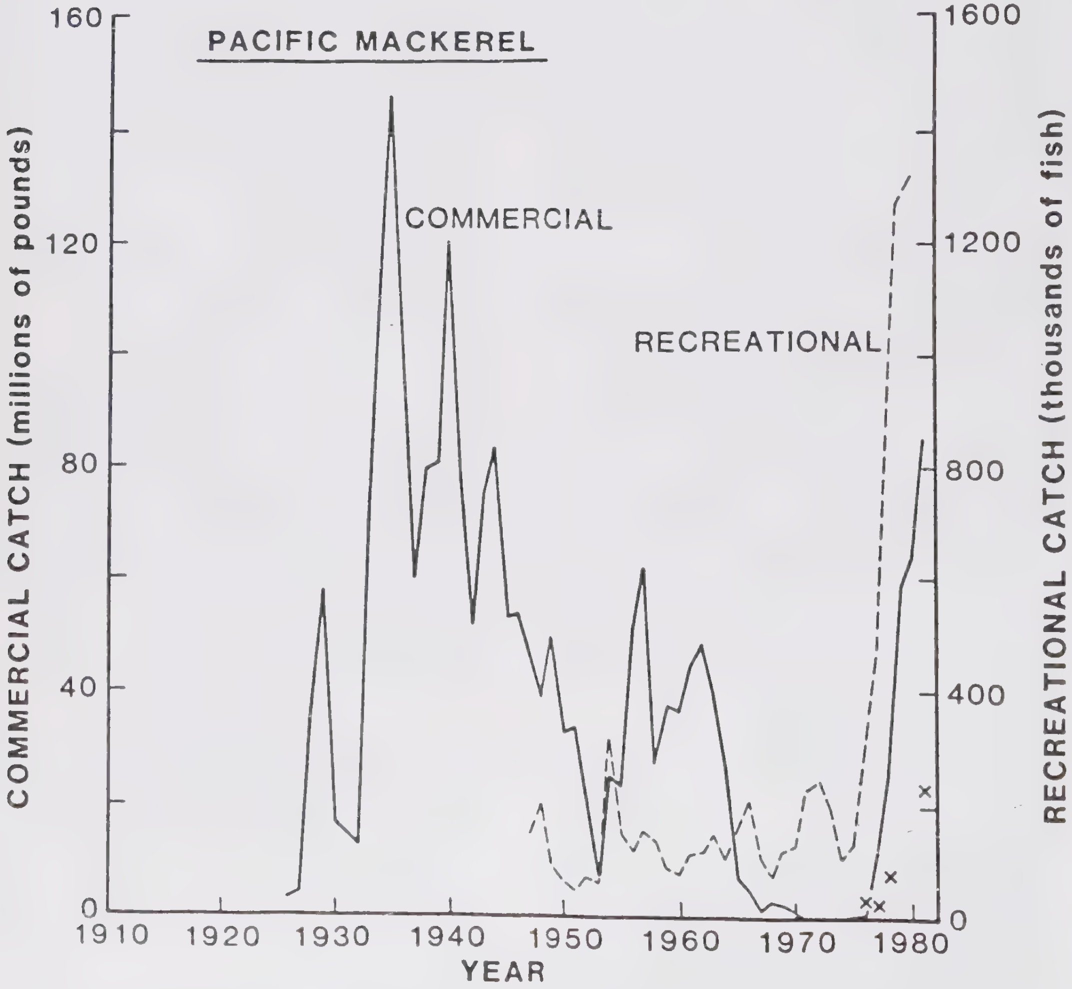

Figure 1. History of the chub (Pacific) mackerel *(Scomber japonicus)* fisheries. The solid line is the total harvest by commercial fishermen. The dashed line is the harvest by commercial passenger fishing vessels. The X's are harvests by independent sport fishermen.

10,000 tons. The allowable quota was set at 20% of the spawning stock over 10,000 tons and 30% of the spawning stock over 20,000 tons.

During the mid-1970s, large numbers of chub (Pacific) mackerel were found schooling with jack mackerel. Commercial "wetfish" fishermen complained that compliance with the 18% incidental catch tolerance was at best difficult and probably unnecessary. In June, 1977, urgent legislation temporarily increased the tolerance factor to permit continued fishing for jack mackerel without capturing illegal quantities of chub mackerel. CDFG biologists determined that the stock level was above the cut-off point and, in January, 1978, the first chub mackerel quota of 5000 tons was established for the 1977-1978 fishing season. This quota was harvested and, in July, 1978, new legislation changed the quota formula to one based on total stock rather than spawning stock (thus increasing the 1977-1978 quota from 5000 to 9300 tons). It also gave the Director of CDFG more discretion in setting the incidental catch tolerance factors and in adjusting quotas as new information became available.

The 1978-1979 quota was set at 14,000 tons and later raised to 18,000 tons based on new biological data. The Director set various trip limits and other restrictions to distribute this quota over as long a period as possible. The 1978 legislation was set to expire in 1981 and, in the summer of 1980, the California Assembly enacted Assembly Bill 2194 which defined the fishing season, the limits of the stock, and the quota formula (including a moratorium when the stock level is below 20,000 tons). It directed the CDFG to determine the stock level, set the quota, monitor the catch, and establish incidental catch tolerance factors after the quota has been harvested.

In retrospect it seems that the original legislation in 1970 and 1972 was close to the mark. By establishing a moratorium and limiting catches during the early stages of the recovery, it probably allowed the resource to recover to a sufficient level from which it could explode to the high abundance of 1979-1980. The major shortcoming of the 1970-1972 legislation seems to be that it did not give the Director of CDFG sufficient flexibility to adjust incidental catch allowances during the transition period when Pacific mackerel were increasing in abundance. A similar situation could soon arise with another species, Pacific sardine *(Sardinops sagax)*, that has been at low abundance and protected by a moratorium for many years. In recent years their incidence in loads of other "wetfish" has greatly increased. If the sardine increase substantially in abundance, the chub (Pacific) mackerel experience will provide a useful precedent. Recovery of a resource could easily be "nipped in the bud" if too large a fishery is allowed too soon.

It is interesting to note that the management guidelines established by the California Assembly differ greatly from the optimum yield guidelines specified in the Magnuson Fishery Conservation and Management Act of 1976. The goal of the Assembly Bill 2194, in 1980, was ". . . that [chub] mackerel be maintained at a total population above 20,000 tons in specified waters" and dictated a quota formula to accomplish this goal. The biological and economic data required to achieve that goal are much fewer than those required to harvest the stock optimally. Optimality is a difficult state to define for a highly fluctuating resource. The goal defined by the California Assembly is both pragmatic and realistic.

The chub (Pacific) mackerel resource and its management regime seem to be healthy. The stock is relatively abundant and a quota formula is in effect to prevent overfishing. The commercial fishery is conducted primarily by the old and rather stable "wetfish" fleet so great pressure to expand the fishery is not anticipated.

The potential future trouble spots are few. Should the Mexican fishery for chub (Pacific) mackerel greatly increase, an international team of fisheries scientists probably should be established to define better the stock structure and determine to what extent the two fisheries compete for the same resource. A resurgence of sardines and attendant incidental catch in the chub mackerel fishery could lead to legal conflicts. Finally, the meteoric rise in this stock's abundance could be followed by an equally rapid natural demise. Assembly bill 2194 makes no explicit mention of natural stock variability. Fisheries managers and commercial fishermen should not be blamed if the stock level does not remain above 20,000 tons.

Pacific Bonito

A commercial fishery for bonito has existed throughout this century but large commercial landings did not occur until 1966 when market demand increased. Bonito are fished by local "wetfish" seiners and by large tuna seiners fishing along southern Baja California after tuna fishing trips. Bonito have occasionally been a large component of the recreational fishery but this catch is much smaller than the commercial catch. In 1981, local purse seiners harvested 10.8 million lbs., U.S. tuna purse seiners harvested 5.7 million lbs. off Baja California, the CPFV fleet landed 0.99 million lbs., and the independent sport fishermen landed 0.26 million lbs.

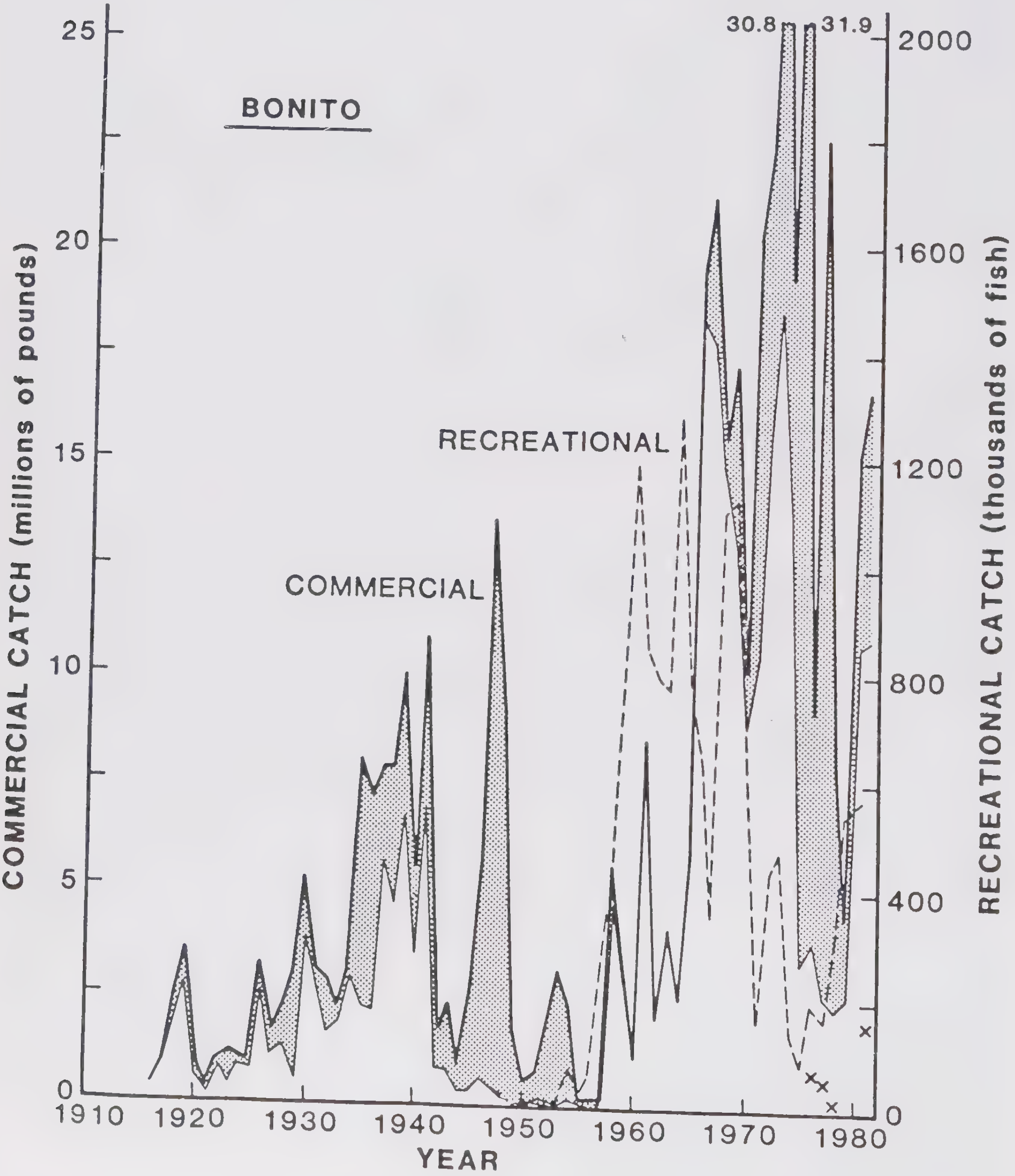

Figure 2. History of the Pacific bonito (*Sarda chiliensis*) fisheries. The solid line is the total harvest by commercial fishermen. The dashed line is the harvest by commercial passenger fishing vessels. The X's are harvests by independent sport fishermen. The shaded region indicates the portion of the U.S. commercial harvest made in Mexican waters.

Collins et al (1980) identified two segments of the bonito stock. The northern segment is composed of young fish that remain in southern California waters through their first spawning season. These small fish support the U.S. recreational fishery and were increasingly exploited by the local commercial fishery after 1975. The southern segment is composed primarily of larger fish that migrate annually from southern Baja California into U.S. waters. When available in U.S. waters, these fish attract the commercial fishery.

There are two sorts of fluctuations in the landings of bonito: total landings and fractions of landings that occur in U.S. waters. Total landings have ranged from four to 32 million lbs. since expansion of the commercial market in 1966, and were greatest during 1973-1975 (Fig. 2). The transboundary distribution of the catch has fluctuated even more. Less than 10% of the commercial catch came from U.S. waters during the years 1946 to 1954. Greater than 98% came from U.S. waters during 1959 to 1965. Since 1971, the U.S. fraction has fluctuated between 11 and 73%. The recreational catch and catch-per-unit-of-effort in U.S. waters have fluctuated similarly to the fluctuations in the U.S. fraction of the commercial catch (Collins et al 1980).

Large commercial catches in U.S. waters probably are dependent on the availability of fish from the southern segment. It seems that the extent of the annual migration of the southern segment is influenced by ocean temperature. When the ocean is warm (e.g., 1958 to 1960) a larger fraction of the southern segment moves into U.S. waters. This variable migration of the bulk of the population will complicate evaluation of management of this species. Even with effective management, there will be occasional periods of low availability in U.S. waters that may persist for several years.

The bonito fisheries were substantially unregulated during the years of expansion. In response to declining southern California catches during the mid-1970s, and expecially to a lack of large fish, a state-federal team of fisheries scientists was assembled to evaluate management options. According to the team (Collins et al 1980):

> The overall goal of bonito management is to achieve an optimal long-term balance among the following specific objectives:
>
> 1. Ensure the reestablishment and maintenance of bonito in southern California,
> 2. Enhance the recreational catch of bonito in southern California,
> 3. Enhance the long-term yield from the U.S. commercial fishery, and
> 4. Reduce conflicts between recreational and commercial fishermen.

The team studied the population dynamics of bonito and considered six management options. Three of these options—area closures, season closures, and revision of U.S. yellowfin tuna regulations—were rejected by the team as ineffective. Area and season closures are ineffective because of the variable timing and location of the annual appearance of bonito in southern California. Revision of the tuna regulation was considered because bonito are often harvested along Baja California to top-off tuna loads. However, the team's analysis indicated that most of this top-off was not due to efforts to increase the allowable incidental catch of yellowfin tuna during its closed season. The team concluded that bonito were being harvested for their own market value, and a change in the yellowfin regulations would have little effect on bonito harvest at the end of yellowfin fishing trips.

The team recommended three options—catch quota for the commercial fishery, size limit in the commercial fishery, and a bag limit for the recreational fishery. Catch quotas were recommended to reduce fishing mortality and improve the status of the southern California segment of the stock. An earlier population model also indicated that bonito were being exploited at or beyond the level of maximum sustainable yield (MacCall, Stauffer, and Troadec 1976). A size limit of five lbs. or 24 inches was recommended for the commercial fishery. This would allow the fish to spawn at least once before entering the fishery and would reduce direct competition between commercial and recreational fishermen for the smaller fish. The team also considered a size limit of three lbs. This limit would have resulted in greater short-term yields but a severe reduction in the spawning stock and consequent long-term yields. Additionally, fish are near the size of three lbs. during the fishing season so enforcement problems were anticipated. Thus the team's preference for a five lb. size limit was based on both biological and practical considerations. A size limit on the recreational fishery was considered unnecessary because of the small magnitude of the recreational harvest and impractical because of the small size of fish typically landed by sport fishermen. Instead the team recommended a recreational bag limit, especially during years of low abundance.

In 1980, the California Legislature enacted a bill that established a size limit of five lbs. or 24 inches on the catches of the commercial and recreational fishery. No catch quota was established. Although the team's analysis did not indicate the need for a size limit on the recreational fishery, political considerations required regulations that have roughly equal impact on all resource users. Both fisheries were given tolerances for undersized fish. The commercial purse seiners were allowed 18% by weight of their load to be undersized fish. The recreational allowance was two undersized fish during winter months and five undersized fish during the summer when young of the year fish are common. Because the daily bag limit is 10 fish, the winter tolerance is 20% by number when full limits are landed.

The size-limit legislation is set to expire in 1985. During the intervening time, the effect of the regulation will be monitored. The eventual question will be: Has the resource recovered? Evaluation of that question with only five years of information will be difficult. Year-to-year variability in the portion of the stock available to U.S. fishermen is great. Changes in oceanographic conditions could bring a large portion of the southern segment into U.S. waters and confound analysis of changes in the local segment. More biological information on the relation between the northern and southern segments of the stock is desperately needed and difficult to obtain. With more data and a concerted analytical effort, there is a chance that the southern segment's migration could be predicted from oceanographic conditions.

The establishment of the size limit should greatly reduce the commercial fishery's harvest of small fish. This may improve recreational fishing in U.S. waters. In 1982, the Mexican government did not grant licenses for U.S. fishermen to harvest bonito in Mexican waters. This was primarily because of a dispute over tuna fishing. The results of the exclusion could be beneficial if this fishing effort disappears, or detrimental if it shifts to U.S. waters. Most of the excluded vessels are long-range tuna seiners that are unlikely to fish locally. Further declines in bonito abundance should trigger reconsideration of the state-federal team's (Collins et al 1980) recommendation that a quota formula—perhaps similar to that for chub mackerel—be established. However, until information on the stock in Mexican waters and the Mexican harvest are incorporated in the analysis, we can only regulate the U.S. fishery. Management of the total resource requires biological information and cooperation with the Mexican government.

California Halibut

The California halibut has supported a commercial and recreational fishery throughout this century. The otter trawl was the traditional commercial fishing gear but entangling nets recently have dominated the fishery. The recreational fishery is conducted with hook and line using rather specialized techniques so incidental catch of other species is low. Little is known about the life history and population dynamics of this species.

Commercial landings of halibut in California have fluctuated greatly (Fig. 3). Periods of relatively high catch occurred during 1916 to 1922, 1944 to 1949, 1962 to 1968, and 1979 through 1982. The amplitude of these high catches declined during 1916 to 1950. The trend is not evident since 1950. The high catch of 1981, 1.2 million pounds, is similar to the high catch of 1964 to 1965, 1.1 million pounds. Additionally, the low catch of 1969 to 1974, about 0.3 million pounds is similar to the minimum during 1958 to 1960.

Recreational landings data from CPFV are available since 1947 and indicate the same peaks and valleys as the commercial landings until the early 1970s (Fig. 3). The recreational catch was about 40% of the commercial catch during the period from 1947 to 1970 (assuming four lbs. per fish; Karpov 1981). The recreational catch declined substantially since 1970 and, by 1976, the commercial catch increased to about eight times the recreational catch. During this period independent sport fishermen increased their proportion of the sport catch. CPFVs cannot profitably target on scarce halibut because the incidental catch of other species is low.

Two regulations historically have affected the commercial halibut fishery: exclusion of trawls

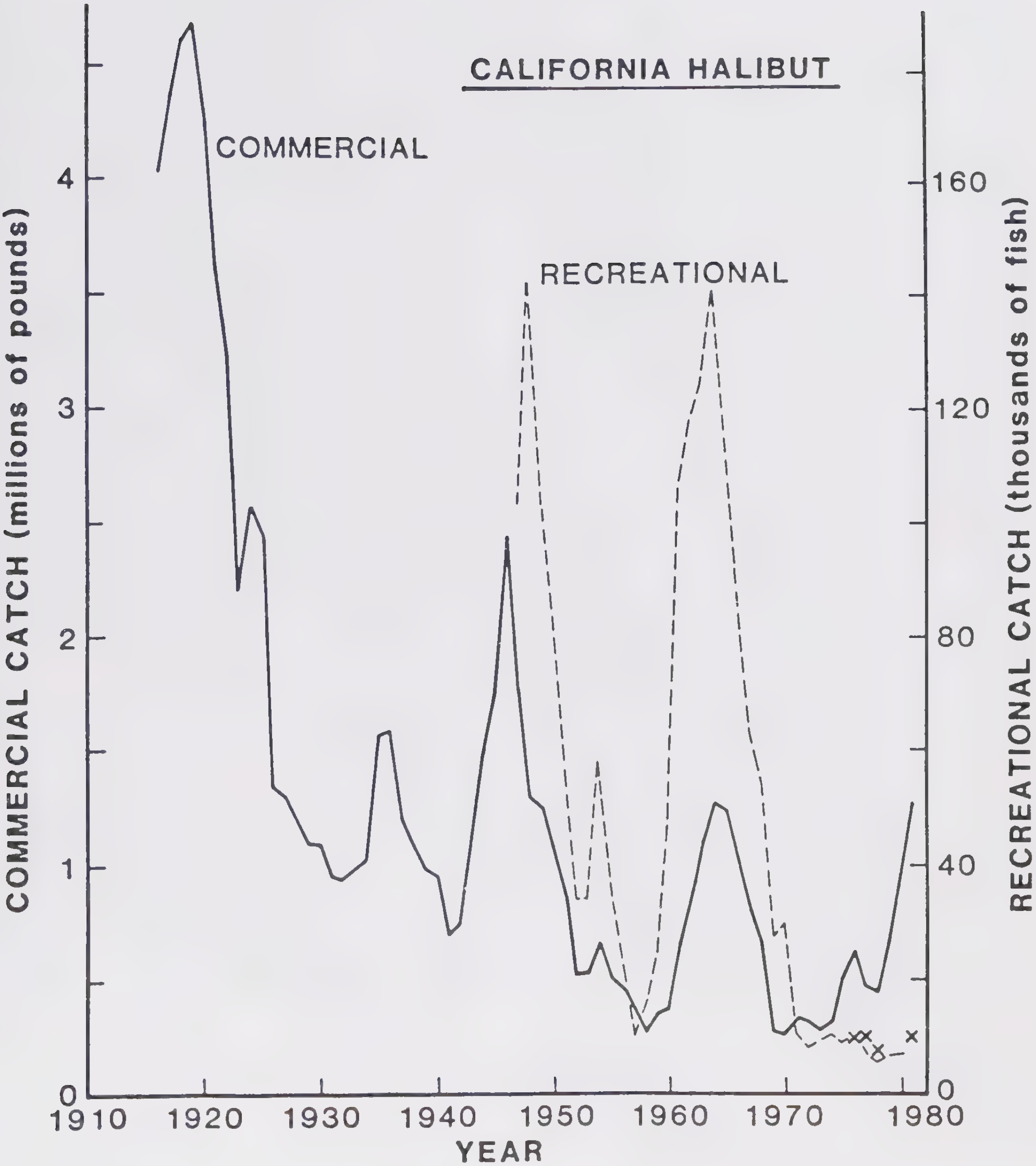

Figure 3. History of the California halibut *(Paralichthys californicus)* fisheries. The solid line is the total harvest by commercial fishermen. The dashed line is the harvest by commercial passenger fishing vessels. The X's are harvests by independent sport fishermen.

from the region nearshore of three miles and a four-pound size limit. Because the preferred habitat of halibut is shallow sandy bottoms, much of the stock was unavailable to the trawl fishery. During the low catch period of the late 1960s, there was interest in increasing short-term catches while allowing gradual improvement of the resource. In 1971, the California Assembly attempted to improve catches by establishing a special inshore halibut trawl ground that extended to one mile off shore in the Santa Barbara area.

To allow gradual improvement of the stock, special regulations were placed on trawling in this region. The season was closed from March 15 to June 15 and a minimum mesh size of 7.5 inches was required in the cod end of the trawls. The closed season was designed to protect the nearshore fish during the spawning season. The mesh-size limitation was designed to permit undersized fish to escape through the mesh (Schott 1975). At the same time, a 22-inch size limit was established for the recreational fishery to balance the regulatory impact between the commercial and recreational fisheries. The biological impact of opening the nearshore region to trawling was balanced against the increased protection of the young fish.

The legislation that established the halibut trawl grounds also required that the effect of the legislation be evaluated. Schott (1977) found that the mesh-size regulation was effective in greatly reducing retention by trawls of fish less than 22 inches (about four pounds). Compliance with the recreational size limit initially was poor but now is improving. In 1975 to 1976 greater than 43% of the halibut landed by the independent sport fishery were smaller than legal size but, by 1981, this figure had declined to less than 29% (Wine 1979b, 1982). Although an attempt to detect a recovery in the stock was inconclusive (Karpov 1981), the commercial catch increased greatly in 1981 after the report was prepared.

The current status of the California halibut resource is uncertain. It may be true that the increased protection of the small fish is responsible for the recent increase in commercial catch. It is equally possible that another natural cycle in halibut abundance is underway, similar to the cycles that seem to have occurred over several decades (Fig. 3). A third possibility is that the shift from trawls to gill nets (see below) has changed greatly the availability of the stock to fishery. The failure of the recreational fishery to recover may also indicate that the gear availability change is the important factor. However, the recreational fishery is now under control of a size limit that certainly is reducing catch and may be reducing interest and effort. Proper evaluation of the effect of the halibut trawl-ground legislation will require monitoring the stock throughout the present cycle of catch, perhaps longer.

During the 1970s, there was a complete change in the relative importance of otter trawls and entangling nets in the halibut commercial fishery. In 1971, 83% of the commercial catch was by otter trawl. In 1981, this proportion had decreased to 21%. Set gill nets and trammel nets had become the dominant commercial fishing gear. This shift probably has two major causes. One likely cause is the set of restrictions placed on the commercial trawl fishery (area closures, season closure in the special trawl ground). The other is the high cost of trawling relative to fishing with entangling nets from small boats. Entangling nets are effective and efficient and their current use for halibut is largely unregulated. Less than 10 years after the California Assembly enacted the halibut trawl ground legislation to improve management of the halibut fishery, the nature of that fishery has changed in such a way as to nullify the effectiveness of the regulations. Information on the fishing power of entangling nets of various mesh sizes will be required before equivalent regulations can be established.

White Seabass

The white seabass has probably the longest and most complicated history of management of any marine species in California (Collins 1981, Vojkovich and Reed Ms.). The commercial and recreational fisheries for seabass are 100 years old; the first regulations were enacted in 1931. Commercial fishermen have used purse seines, various entangling nets, and hook and line to harvest seabass. The early fishery was conducted primarily with purse seines but this became uneconomical as abundance declined. Purse-seine fishing for white seabass was prohibited in 1939, and today's fishery is primarily by set gill net.

The commercial catch of white seabass declined steadily during the 1920s and 1930s (Fig. 4). San Francisco was the principal early port of landing but, as catches declined, the northward limit of catches retreated southward. There was no further decline during the next two decades. Then, during the warm-water period of 1958 to 1960, there was a tremendous increase in the catch in U.S. waters. The entire population apparently shifted northwards, because catches in Mexico were at record low levels and white seabass were captured as far north as Alaska. Immediately following the warm-water period, the catch in U.S. waters returned to its former

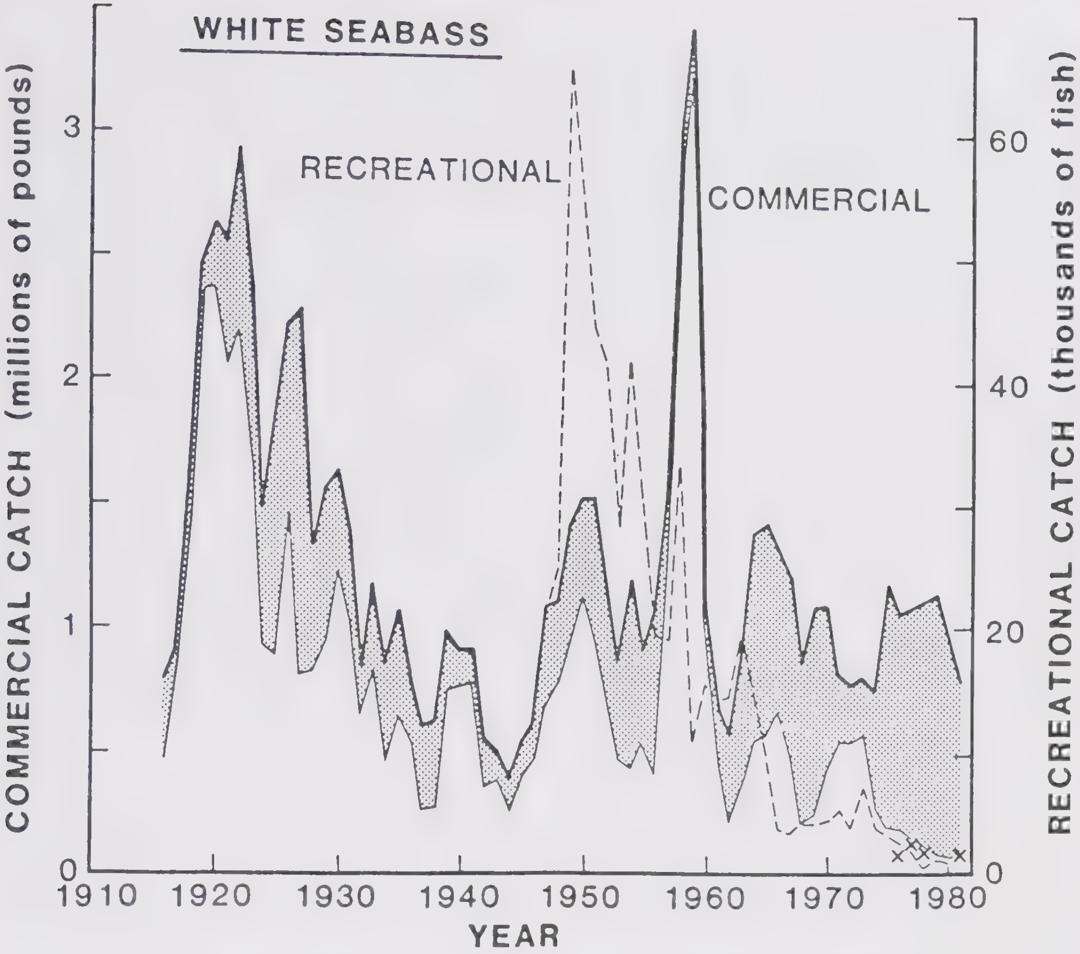

Figure 4. History of the white seabass *(Atractoscion nobilis)* fisheries. The solid line is the total harvest by commercial fishermen. The dashed line is the harvest by commercial passenger fishing vessels. The X's are harvests by independent sport fishermen. The shaded region indicates the portion of the U.S. commercial harvest made in Mexican waters.

level, then continued to decline slowly during the 1960s. The commercial harvest by U.S. fishermen in Mexican waters exceeded their catch in U.S. waters during the 1960s and 1970s. The catch in U.S. waters declined steadily during the late 1970s and is now at the lowest level since record-keeping began.

The recreational fishery developed later than the commercial fishery and peaked in the late 1940s (Fig. 4). Abundance probably was relatively high at that time because the commercial fishery also had a minor peak during the late 1940s. Recreational catches declined precipitously after the peak. There was little increase in recreational catch during the warm-water years. Catches are at an extremely low level today.

Management of the white seabass has a long history. Several types of restrictions have been applied to the commercial and recreational fisheries (Collins 1981, Vojkovich and Reed Ms.). In the 1930s, a 28-inch size limit was established, the season was closed to net fishing during the spawning season, and other gears had trip limits imposed. The latter restrictions were substantially removed in 1939 when purse seining was outlawed and gill nets were required to have a minimum mesh size of 3.5 inches. Year-round commercial trip limits were reimposed in 1953 and, in 1980, the spawning season (March 15 to June 15) was closed both to commercial and recreational fishing. Bag limits for sport fishermen were set at 15 fish per day in 1937, then reduced to 10 per day in 1949, and to three per day in 1980.

The earliest regulation imposed on the fishery was the minimum size limit of 28 inches. Since its enactment in 1931, the only aspect of this limit that has changed is the allowable retention of undersized fish by sport fishermen. In 1949, five undersized fish were allowed. The allowance declined to two fish in 1957, none in 1971, one in 1973, and back to none in 1978. At current low levels of recreational catch, any allowance for undersized fish negates the effectiveness of the size limit because anglers rarely catch more than one seabass per day.

Enforcement of the size limit on the recreational fishery has been difficult because private anglers typically cannot identify juvenile white seabass. In 1976-1977, only 6.6% of the independent sport fishermen's seabass catches were of legal size (Wine 1978) and 22% of the interviewed fishermen could not correctly identify adult white seabass (Hartmann 1980). Identification of juveniles was even more of a problem. Fortunately the sublegal catch by independent sport fishermen has been declining in recent years. The problem is much less severe on CPFV where the experienced crew assist in identification. Clearly, if size and bag limit regulations are to be effective the public must be educated. The California Department of Fish and Game is preparing an education program to improve identification of sport fishes.

The recreational and commercial fisheries differ greatly in the size of fish captured. The commercial fishermen typically use set gill nets with large (6.5-inch) mesh and capture large fish that are in highest demand in the market. Sport fishermen in the same area rarely capture large fish and typically capture many sublegal white seabass (Vojkovich and Reed Ms.). It is not known whether the size distribution in the recreational harvest indicates the true relative abundance of large and small seabass or if some behavioral characteristic makes the large fish less available to the sport fishermen. It is interesting that the recreational fishery, which is based on small fish, has declined recently much more than the commercial fishery based on large fish. This pattern is opposite that expected in a typical overfished resource: one expects older fish to disappear first. Collins (1981) speculates that the large fish in California waters may migrate from Baja California and that all of them may not be the progeny of local spawn. If true, this may explain the only minor increase in recreational catch during the warm-water years, 1958 to 1960. The fish that moved north, and enhanced the California commercial fishery, may have been too large to be completely available to the sport fishermen. More information on migration along shore is clearly necessary if white seabass in California are to be managed properly. Cooperation with Mexican scientists and the Mexican fishery is a necessary step towards obtaining this information.

Three studies have been conducted in response to perceived declines in white seabass abundance. Clarke (1930) studied age at first maturity; it was on the basis of this work that the 28-inch size limit was established. Following the decline in recreational catches during the 1950s, a study of ages of fish in the catch and status of the stock was conducted (Thomas 1968). The study concluded that the stock was in good health but the harvests continued to decline. Collins (1981) points out that most of the data were collected during the abnormally warm years, 1958 to 1960, when the stock was shifted north and availability was high. The misreading of the true status of the stock by the Thomas study *(op. cit.)* should serve as a warning against uncritical reliance on short-term studies to evaluate the effect of changes in management. The five-year period usually established by the California Assembly for such evaluations is too short and will be heavily influenced by the particular environmental events occurring during that period. If evaluation of management must occur within five years, then monitoring of stock levels is insufficient. Detailed and extensive studies of the processes involved (age-specific mortality, growth, reproduction, and migration) will be necessary to evaluate the changed fishery regulations.

The third study was conducted during the 1970s. By then, the recreational catch was so small that collection of sufficient specimens for biological studies was difficult (Maxwell 1977). The recommendations from that study were to prohibit sport fishermen from keeping any undersized fish, to close the commercial fishery during the spawning season, and to raise the minimum size of 32 inches. The first measure has been enacted, the second was modified and enacted, and the third is under consideration, pending evaluation of the effect of the first two measures.

The white seabass resource in U.S. waters is badly depleted at present. It is too early to evaluate the effect of efforts to eliminate the recreational harvest of sublegal fish. However this stricter regulation has little chance of succeeding unless the public first learns how to identify juvenile seabass. U.S. commercial fishermen were not permitted to fish in Mexican waters during 1982. If this situation continues, and that fishing effort disappears, the effect on the total stock should be beneficial. If that effort is merely diverted into U.S. waters the local effect could be disastrous.

The great increase in U.S. catch during warm-water years (1958 to 1960) and the anomalous size distributions mentioned by Collins (1981) suggest that white seabass occurring in U.S. waters are but the fringe of a larger and perhaps healthier stock in Mexico. Whether U.S. fish originate largely in Mexican waters has a great influence on needs for further restrictions on U.S. harvests. More biological information on migration needs to be collected.

Summary

Four of California's nearshore fish species, having different biological and managerial histories and problems, have been discussed. Several basic problems stand out: great natural fluctuations in stock levels, the transboundary distribution of most of these stocks, excess effort in the commercial fishery, and poor knowledge of species identification and fishing regulations among sport fishermen.

The problems of fluctuations in stock abundance and the transboundary distribution of the stock are intimately confounded. Changes in oceanographic conditions that affect natural survival and reproduction also affect movements of the stock along the coast. The possible interactions are complex. Warm water may cause a larger portion of a stock to move into U.S. waters while being detrimental to reproduction of the bulk of the stock residing in Mexican waters. Thus, biological information collected in U.S. waters would indicate an increasing stock when, in fact, poor reproduction is leading to a decrease in stock abundance. A problem of this type may have occurred with white seabass during the warm-water event of 1958. In general, natural fluctuations in stock abundance complicate evaluation of changes in management. When stocks are declining, public pressure to restrict the fisheries increases. By the time new regulations are enacted, the stock may be in a natural recovery and evaluation of the new regulations is difficult. The fact that regulations typically apply only to U.S. fishermen while in U.S. waters is a sufficient problem. The situation is even more difficult because most of the biological information for monitoring the fishery also comes only from U.S. waters. Establishment of international teams of scientists should be encouraged and their recommendations should guide further management efforts.

The problem of excess fishing effort varies among the four species examined here. The chub mackerel fishery is most strictly regulated by an annual catch quota that is a proportion of the stock size. Restrictions on the fisheries for California halibut, bonito, and white seabass include outlawing certain gear, restricting other gear, and size limits on the commercial and recreational fisheries. A problem with specific gear restrictions is the difficulty of balancing the regulatory impact among all users. As regulation of the halibut trawl fishery increased, the effort shifted to the relatively unregulated gill-net fishery. Size limits and associated gear restrictions that reduce the take of young fish by the commercial fishery are workable regulatory measures. Whether they will be sufficient to halt the decline of white seabass and bonito remains to be seen. Compliance with size-limit regulations among independent sport fishermen has been poor. Public education in species identification seems a useful approach.

Acknowledgments

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Richard Methot is a fisheries biologist with the National Marine Fisheries Service at La Jolla, California. Dr. Methot's academic background includes a B.S. degree in fisheries from the University of Washington in 1975 and a Ph.D. in biological oceanography from Scripps Institution of Oceanography, University of California, San Diego in 1981. Dr. Methot has worked on growth and mortality of larval fishes, population dynamics of Dungeness crab, and is now working on anchovy population dynamics and management.

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SEASONAL VARIATION IN SURVIVAL OF LARVAL NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, ESTIMATED FROM THE AGE DISTRIBUTION OF JUVENILES

RICHARD D. METHOT, JR.[1]

ABSTRACT

Juvenile northern anchovy, *Engraulis mordax*, collected during autumn of 1978 and 1979 were aged using daily increments in their otoliths. Neither year class was dominated by individuals born during some short period, but March and April had the highest frequency of births in each year. Monthly ichythoplankton surveys indicated that significant spawning occurred from January through May of each year and peaked in early March. Comparison of the temporal distribution of birth dates with larval abundance indicated that larval survival was similar in the first half of each spawning season and greater during April to May of the 1978 spawning season than the same period in 1979. This difference in seasonal pattern of survival was nearly sufficient to account for the observed greater recruitment in 1978 and is consistent with the hypothesis that offshore transport of larvae influences recruitment.

One goal of fish population dynamics is to understand the processes responsible for annual variation in recruitment. The variation can be more than an order of magnitude and is poorly correlated with abundance of spawners (Cushing and Harris 1973). The concept of a critical period during the early larval stage (Hjort 1926; Marr 1956; May 1974) has structured much of the research. Recent work has focused on the importance of temporal and spatial coincidence of first feeding larvae and concentrations of prey (Beyer and Laurence 1981; Lasker 1978; Vlymen 1977). However, transport of larvae away from juvenile nursery areas can influence recruitment (Nelson et al. 1977; Parrish et al. 1981) and the role of predation is unknown.

Seasonal variation in factors that cause annual variation in recruitment probably influences the average timing of spawning. Support for this hypothesis comes from the latitudinal correlation between duration of the spawning season and the plankton bloom (Wyatt 1980). More direct evidence is found within the North Sea where the short spawning season of each herring population bears a fixed phase relation to the mean date of the local plankton bloom (Cushing 1975). The timing of the most favorable environmental conditions may not be predictable in each year. The match-mismatch hypothesis (Cushing 1975) suggests that variation in the relative timing of spawning and the seasonal plankton bloom contributes to variation in recruitment.

Collection of sufficient years of data to test any recruitment hypothesis is difficult. However, a testable corollary of Cushing's hypothesis is that, in any year, larvae born during favorable environmental periods constitute most of the year class. The age distribution of juveniles—the survivors of the larval stage—is a function of the seasonal distribution of spawning and seasonal changes in larval survival. To test the match-mismatch hypothesis, the birth dates of juvenile northern anchovy, *Engraulis mordax*, were determined from daily increments in otoliths (Brothers et al. 1976; Methot and Kramer 1979; Pannella 1971) and compared with the seasonal distribution of spawning determined from ichthyoplankton surveys conducted during the 1978 and 1979 spawning seasons.

METHODS

Larval Abundance

The seasonal distributions of the northern anchovy larval abundance were estimated from ichthyoplankton surveys (Kramer et al. 1972) on the sampling grid (Fig. 1) of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). Seven surveys were conducted between December 1977 and August 1978 and four surveys between January 1979 and May 1979. Only larvae from 2.6 mm (live standard length at hatch) to 5.1 mm (few days after yolk absorption and onset of feeding) were used in the analysis.

Each cruise's larval census was the summed abun-

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[1] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038.

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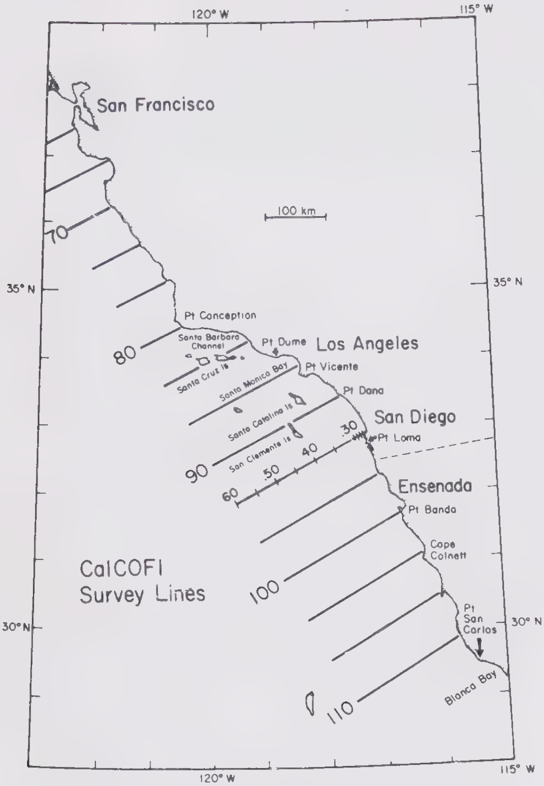

FIGURE 1.—Geographic region inhabited by the central population of northern anchovy. Ichthyoplankton samples were collected along CalCOFI survey lines. Location of stations is indicated only on line 93.3. Samples of juvenile anchovy were collected along the mainland coast. In 1978 these samples were obtained from the bait fishery from Pt. Conception to the United States-Mexico border. In 1979 samples were collected with a midwater trawl from Pt. Conception to Blanca Bay.

dance along CalCOFI lines 60-110. The catch at each station was adjusted for volume of water filtered and weighted by the distance to adjacent stations along the line. Abundances along unsampled lines were estimated from abundance in adjacent lines and cruises. A more complete description and further analyses of these data are in Hewitt and Methot (1982).

The mean and variance of date of larval catch were calculated for each cruise. Each station's contribution to these statistics was weighted by the distance to adjacent stations and by the catch of larvae. The effective duration of each cruise was considered to be ±2 standard deviations of catch date.

Juvenile Northern Anchovy Samples

During the period 28 October-14 December 1978, 30 samples of northern anchovy were collected from bait receivers at sport fishing docks from San Diego to Pt. Conception, Calif. A total of 1,101 fish were measured, but sample size varied from 11 to 86 fish so each fish's contribution to the overall size distribution was weighted by the inverse of sample size. From 15 of the 30 samples, 141 fish were aged using daily increments in otoliths.

During 1-19 November 1979, specimens were obtained from samples taken with a 15 m midwater trawl on a survey conducted by the California Department of Fish and Game (CFG) to investigate the abundance of juvenile northern anchovy (Mais 1980). Trawls were taken parallel to the coast between the 30 and 90 m isobaths at 7.4 km coastwise intervals between Blanca Bay, Baja California, and Pt. Conception, Calif. Past trawl surveys indicate that the juveniles are concentrated into the nearshore zone (Mais 1974). A total of 2,356 fish were measured from the 93 positive trawls; sample size typically was 25 fish per trawl. In addition, 10 of the 25 fish per trawl were aged by CFG personnel using annual growth marks in otoliths (Collins and Spratt 1969). Juveniles are defined here as those fish with no otolith annuli. The fraction of fish with no annuli in each 5 mm size interval was calculated (Table 1). From 8 of the 93 samples, 129 fish were aged using daily increments in otoliths.

Size distributions were calculated in each of three alongshore regions: North of Pt. Dume (north), San Diego to Pt. Dume (central), and south of San Diego (south). These regions were selected on the basis of the distribution of samples in 1978 and minima in the

TABLE 1.—Frequency of northern anchovy with and without otolith annuli. Specimens were collected by trawl during November 1979 (Mais 1980). Results are stratified by region and 5 mm size interval.

Size interval (mm)		North of Pt. Dume		San Diego-Pt. Dume		South of San Diego	
	N annuli:	0	>0	0	>0	0	>0
50						1	
55				4		9	
60		1		7		3	
65		0		12		6	
70		2		11		18	
75		3		28		59	
80		8		23		50	
85		6		13		41	
90		12		8		41	
95		4		4	1	26	26
100		5		5	6	3	71
105		3	5	4	23	2	73
110		2	19	1	66	2	45
115		1	33	1	33		18
120			17		21		3
125			22		8		1
130			7		6		
135			5		5		
140			1				
145			4				

alongshore distribution of juveniles in 1979 (Methot 1981). The regional breakdown was necessary because the overlap in size between juveniles and older fish varied latitudinally (Table 1). Although data in Table 1 are entirely from 1979, they were used to calculate juvenile size distributions from overall size distributions in both 1978 and 1979. In 1978 few adults were collected and no comparable samples were obtained from south of San Diego.[2]

Otolith Preparation

Thawed specimens were measured to the nearest 1.0 mm standard length. Sagittae (largest otoliths) were removed, cleaned in distilled water, dried, and mounted on a microscope slide with a clear methacrylate-based mounting medium. Otoliths of northern anchovy larger than about 40 mm are too thick to transmit sufficient light for viewing the increments. Material was removed from the otolith's medial surface by applying 5-10% HCl to selected regions for about 10 s at a time. Immersion oil, petroleum jelly, or mounting medium were used to mask the outer edge of the otolith and regions already sufficiently thin. The selectively etched surface develops high relief but a thin layer of immersion oil renders this relief nonrefractory and permits examination of the otolith. After most increments became visible, the mounting medium was softened with 80% ethanol, and the otolith was turned over and remounted. Etching of the lateral surface continued until all increments were visible within, but not necessarily at the surface of, the remaining material.

The otoliths in 1978 were prepared by embedding in polyester casting resin and grinding sagittal sections on 400 and 600 grit wet sandpaper. Selective etching was faster and more successful than grinding.

Age Determination

Specimens used for this study also were used to back calculate juvenile growth and a direct count of all increments in an otolith was rarely made. Instead, age was determined from numerical integration of otolith growth (increment width). Increments were measured with a video camera mounted on a compound microscope, an electronic device which positioned a cursor in the video image, and a microcomputer interfaced to the device. All measurements were made along the longest radius of the otolith (towards the posterior margin). The observer positioned the cursor at the outer edge of an increment and keyed in the number of increments between that point and the previous point while the computer recorded the radius to that increment. Increment width usually did not change rapidly so 2-10 increments of similar size were entered together. Data from different regions along the longest radius were recorded at various stages of the etching process.

Data from both otoliths and several replicate transects per otolith were combined in the calculation of age. Mean increment width was calculated at all points along the longest radius. Etching errors occasionally produced a region in which increments could not be seen. When this occurred, increment width was interpolated from mean increment width in adjacent intervals by a linear interpolation of increment width on radius. Age was calculated from numerical evaluation of the following expression:

$$\sum_{i=1}^{n} \frac{r_i - r_{i-1}}{G(r_i)}$$

where the following definitions and boundary conditions apply:

r_i = set of all radial distances where increment width changed perceptibly
$G(r_i)$ = average increment width between r_{i-1} and r_i
r_0 = otolith radius at onset of increment formation (6.5 μm)
r_n = maximum otolith radius
$G(r_1)$ = typical initial increment width (0.8 μm per increment)
$G(r_n)$ = $G(r_{n-1})$ if $G(r_n)$ not measurable.

The result converges exactly to the count of increments if each individual increment is measured once. The age estimate was accepted if <20% of the age was from interpolated increments. About 3% of the fish were rejected by this criterion. The mean percentage of interpolated increments for the accepted fish was 4.7% and the median was 2.5%. Usually an independent age estimate could be made from each otolith. When fish were stratified into 50-d age intervals, the coefficient of variation of age between otoliths within fish averaged 4.6% in 1978 and 3.5% in 1979. Thus, the 95% confidence interval for a 250-d-old fish was ±14 d.

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[2] Two samples from the Ensenada commercial fishery were provided by G. Broadhead (Living Marine Resources, San Diego). The fish had a similar size/birth-date relation to fish from the bait fishery in the U.S. coastal waters. Because the commercial fishery is biased against small fish, the size distribution of juveniles in Mexico could not be estimated.

The birth dates calculated in this study are actually dates of onset of increment formation. The northern anchovy larvae deposit the first increment at about the end of yolk absorption, the fifth day after hatching at 16°C (Brothers et al. 1976). This is close to the mean age of larvae used to estimate larval abundances so no constant was added to the juveniles' ages when calculating birth dates.

The fish in the present study usually had 150-400 increments but the daily deposition of increments in northern anchovy otoliths has been confirmed only to 100 d in the laboratory (Brothers et al. 1976). The accuracy of my interpretation of daily increments in juveniles was tested by comparing birth-date distributions calculated from early samples with distributions calculated from late samples. The distributions should be indistinguishable if the samples were of the same cohort and mortality during the period was not age selective. In addition to the December 1978 samples used in this study, samples were collected at San Diego in September 1978 and February 1979 (Table 2). The three birth-date distributions were compared by the Smirnov test for differences in cumulative probabilities (Conover 1971, p. 309). The September and December distributions were very similar (maximum difference = 0.105, $P < 0.2$) and the February distribution was also not significantly different from September's (0.243, $P < 0.02$). This test is sensitive to aging errors of the same magnitude as the precision of the ages. If ages of February's fish had been overestimated by 15 d (one-half of fish in each month shifted to the following month) the difference between September and February would have increased to 0.376, $P < 0.1$. A 1-mo error in aging the February juveniles would have made the September 1978 to February 1979 comparison highly significant ($P < 0.01$). I conclude that any bias in aging must be less than about 15 d.

TABLE 2.—Birth-date frequency of juvenile northern anchovy collected at San Diego between September 1978 and February 1979.

		Sept-Oct. 1978	Dec. 1978	Feb 1979
	N samples:	2	2	1
	N fish:	28	19	15
	Length (mm):			
	mean	77.8	76.4	82.1
Month	SD	5.5	6.5	5.9
Jan.		0	2	1
Feb.		3	1	1
Mar.		15	9	4
Apr.		10	6	7
May		0	1	2

Birth-Date Distribution

The selected specimens produce a biased estimate of the juvenile birth-date distribution because they were selected to span a wide size range for an analysis of seasonal patterns of juvenile growth (Methot 1981). A less biased estimate of the birth-date distribution was obtained from the size-frequency distribution of a large sample of juveniles and a size/birth-date nomograph (Fridriksson 1934; Kimura 1977). In each year's nomograph, birth-date frequencies (by month) were calculated for fish in each 10 mm size interval. All samples within each year were combined in that year's nomograph.

RESULTS

Larval Abundance

The temporal distributions of northern anchovy larvae differed between the two years (Table 3). The maximum abundance occurred in February-March of each year but the peak was greater in 1978. Larvae were much more abundant during May 1979 than during May 1978. The average larva in 1979 was in water 1°C colder than the average larva in 1978 and was further offshore (Table 3). Larval production per 30-d date interval was calculated by numerical integration of the area under the dashed lines in Figures 2 and 3. Total larval production during January-May 1979 was 2.1% greater than during the same period in 1978.

Size and Birth-Date Distributions

In 1978 and 1979 northern anchovy juveniles, collected north of Pt. Dume, were typically larger (Table 4) and had been born earlier (Table 5) than juveniles collected to the south. The size/birth-date nomograms (Table 6) applied to the juvenile size distributions produced birth-date distributions (Table 7) with peaks in March-April for southern fish and

TABLE 3.—Abundance of northern anchovy larvae. Value in parentheses is the fraction of the abundance that was interpolated. *N* samples exclude offshore samples with no larvae. Date, distance offshore, and temperature at 10 m were weighted by larval catch at each station.

Date	*N* samples	Abundance	Distance (km)	Temp. (°C)
1977-78				
Dec. 15	42	448 (0.08)	119	16.3
Jan. 18	70	558 (0.00)	65	15.5
Feb. 25	87	2,367 (0.00)	65	14.9
Apr. 9	74	686 (0.00)	41	15.8
May 26	64	143 (0.00)	44	15.2
June 30	48	26 (0.00)	72	16.1
Aug. 13	20	26 (0.00)	22	18.1
1979				
Jan. 18	33	448 (0.45)	111	14.0
Mar. 2	71	1,524 (0.00)	65	13.9
Apr. 14	34	1,392 (0.40)	113	14.5
May 10	54	653 (0.00)	54	14.8

TABLE 4.—Size distributions of juvenile northern anchovy calculated from size distributions of all fish and size-specific juvenile fraction (Table 1). The percentage of the population composed of juveniles was also calculated (% juveniles). Area is the surface area (square nautical miles) nearshore of the 50 fathom isobath and excludes the shallow area around islands that was not sampled.

		1978		1979		
		north	central	north	central	south
	Area:	476	484	476	484	1,905
	N samples:	9	21	26	41	66
Size	*N* fish:	429	724	460	757	1,333
(mm)	% juveniles:	82.0	98.8	28.0	40.8	54.4
40-49		0.0	0.3	0.0	0.0	0.3
50-59		0.0	1.9	0.0	2.9	2.8
60-69		3.3	17.1	3.1	17.8	3.9
70-79		18.3	45.4	10.1	31.7	27.3
80-89		26.9	27.3	22.5	26.9	41.0
90-99		34.3	7.7	31.8	11.3	22.5
100-109		16.7	0.3	24.8	8.4	1.8
110-119		0.5	0.0	7.7	1.0	0.6

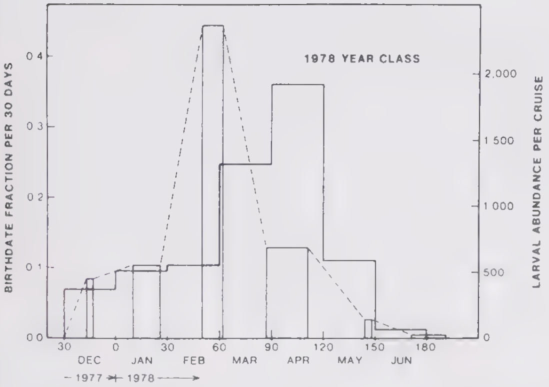

FIGURE 2.—Comparison of the seasonal distributions of northern anchovy larval abundance and birth dates of the 1978 year class. The width of the stippled bars is the effective duration of the ichthyoplankton survey (±2 standard deviations of the sample date where each sample is weighted by its catch of northern anchovy larvae). The dashed line was used to interpolate larval abundance per 30-d period. The open histogram indicates the fraction of juvenile's birth dates occurring per 30 d.

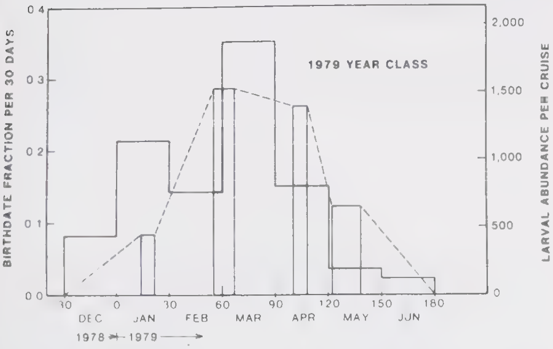

FIGURE 3.—Comparison of the seasonal distributions of northern anchovy larval abundance and birth dates of the 1979 year class. See Figure 2 for explanation.

TABLE 5.—Frequency of observed birth dates of juvenile northern anchovy stratified by year and region and summarized by 10-d date interval.

Date interval		1978		1979		
		north	central	north	central	south
	<−30	3	0	7	1	2
Dec.	−30	2	0	0	0	0
	−20	2	0	2	0	0
	−10	6	0	2	1	0
Jan.	0	1	0	4	1	0
	10	5	2	5	0	0
	20	3	1	3	0	1
Feb.	30	1	4	3	0	0
	40	1	0	1	1	0
	50	6	0	2	3	1
Mar.	60	2	9	0	2	4
	70	0	9	7	7	5
	80	1	6	3	7	5
Apr.	90	2	12	2	7	7
	100	0	14	0	1	0
	110	1	16	0	0	0
May	120	0	10	2	1	1
	130	0	7	2	0	0
	140	0	7	0	0	0
June	150	0	2	2	0	0
	160	0	2	1	0	0
	170	0	0	1	1	0
July	>180	0	4	3	13	2

December-January for northern fish. The calculated birth-date distributions were similar to the observed birth-date occurrences in the two regions in 1978; the calculated differed from the observed in 1979 because selection of specimens was highly nonrandom in 1979. A substantial fraction of 90-110 mm fish in 1979 were assigned to birth dates before December 1978. Because these fish had no otolith annulus they are considered part of the 1979 year class.[3]

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[3] Among the 95-105 mm anchovy examined in 1979, all those with an annulus (1978 year class) had 400-510 daily increments so had been born during summer of 1978. Among the similar-sized fish without an otolith annulus, some had been born in December 1978 and some as early as late summer 1978. This observation indicates the occasional ambiguity of assigning year classes when some spawning occurs throughout the year.

TABLE 6.—Size/birth-date nomograms stratified by 10 mm size interval and 30-d date interval (labeled by approximate month).

Size interval (mm)	Birth month								
	<Dec.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	>June
				1977-78					
40								1	2
50							4	2	1
60			1	0	2	14	10	0	1
70				2	7	20	5	1	
80			4	4	15	10			
90	2	5	4	4	3	1			
100	1	5	3	2					
				1978-79					
30									4
40									6
50								1	6
60					3	0	4	3	2
70				2	19	9	1	1	
80	1	2	7	6	17	8	1		
90	7	3	6	2	1				
100	2	0	1	1					

TABLE 7.—Birth-date distributions calculated from size/birth-date nomograms (Table 6) and regional juvenile size distributions (Table 4) Distributions are presented as %/30-d date intervals (labelled as approximate months). Combined birth-date distribution is mean of regional distributions with weighting factors proportional to nearshore shallow area (Table 4). Mortality correction factor accounts for the greater duration that the early born fish are exposed to juvenile mortality (see text). After multiplying the combined distributions by the mortality correction factors, the distributions are presented only for those months with larval abundance data.

	<Dec.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	>June	Weight factor
Regional distributions:										
1978										
central	0.8	2.1	5.5	7.6	23.7	41.9	15.4	2.0	1.0	83.4
north	5.2	16.8	15.3	14.7	21.5	21.8	4.1	0.5	0.1	16.6
1979										
south	10.5	5.5	14.5	10.5	34.9	15.5	3.1	2.2	3.3	66.5
central	9.5	3.1	10.4	9.3	34.7	14.0	7.6	5.9	5.5	16.9
north	28.5	6.1	21.9	15.4	17.0	7.6	1.9	1.1	0.5	16.6
Combined distributions										
1978	1.5	4.6	7.1	8.8	23.4	38.5	13.5	1.7	0.9	
1979	13.3	5.2	15.0	11.1	32.0	13.8	3.7	2.7	3.2	
Mortality correction factors										
		2.09	1.85	1.64	1.45	1.28	1.13	1.0		
Combined distributions corrected for juvenile mortality										
1978		7.0	9.6	10.4	24.7	35.9	11.1	1.3		
1979		8.5	21.8	14.2	36.3	13.9	3.2	2.1		
1979			24.4	15.9	40.6	15.5	3.6			

Combining the regional results to produce an overall juvenile birth-date distribution is problematic, especially in 1978 when no samples were collected south of San Diego. Each region's weighting factor should be proportional to the abundance of juveniles in the region. Because local abundance of a pelagic schooling fish is measured crudely by a trawl survey, the areas of the primary juvenile habitat (Table 4) were used as weighting factors. The north region has only 16.6% of the total area nearshore of the 90 m (50 fathom) isobath, so contributes little to the total. Although the north region contributed nearly 50% of the total area from which samples were obtained in 1978 (Table 4), I assume that the unsampled fish from Baja California had birth dates similar to those of San Diego-Pt. Dume fish so I use 16.6% for the north's weighting factor in 1978. The combined birth-date distributions are in Table 7.

Correction for Juvenile Mortality

The birth-date distributions for the northern anchovy presented above represent the birth dates of those fish which survived until November. A monthly cohort's contribution to the birth-date distribution of its year class is a function of the spawning rate during that month, the mortality rates experienced by that cohort, and the age of that cohort when sampled. Northern anchovy juveniles which had been born during January are expected to be less abundant in November than juveniles born in May because the older juveniles experienced mortality as juveniles for a longer period. A correction for this difference in age is necessary before differences between the seasonal distribution of larval abundance and the resultant distribution of juvenile birth dates can be interpreted as differences in larval survival. Few juveniles collected in November were <5-mo-old so the relative abundance of older juveniles need only be adjusted by the inverse of survival from age 5 mo to age at capture. Age-specific survival rate was assumed to increase from 64% per month at age 3 mo to 88% at 10 mo (calculated from preliminary estimates of juvenile mortality rates in Smith 1981). If one assumes no seasonality in juvenile survival, the resultant birth-date distributions are as if all the monthly cohorts had been sampled at the same age rather than at variable ages in November. Because most juveniles were between 6 and 10 mo old, corrected birth-date distributions are similar to the uncorrected distributions (Table 7).

Relative Larval Survival

The juveniles' birth-date distributions, corrected for juvenile mortality, and the seasonal distributions of larval production for the northern anchovy are presented in Figures 2 and 3. The ratio of monthly birth-date frequency to monthly larval production is an index of larval survival relative to survival from other months in the same spawning season. Survival tended to increase within the 1978 season and decrease within the 1979 season (Fig. 4). In both years the only anomalies to the trends were low relative survival of larvae born in February.

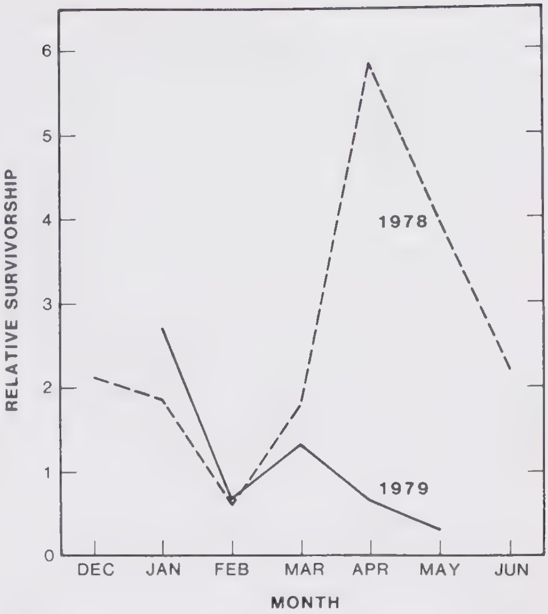

FIGURE 4.—Relative survivorship is the ratio of the fraction of northern anchovy juvenile's birth dates to the fraction of annual larval production per 30 d. To enable comparison between years the relative survivorship for 1978 has been scaled by the ratio of recruitment (2.0) and the ratio of annual larval production (0.98) between the 2 years.

DISCUSSION

This study has documented seasonal changes in survivorship of larval northern anchovy. Both the magnitude and the timing of changes are important. The magnitude of the seasonal changes determines whether annual variation in recruitment could be caused by short seasonal events. The timing of the changes in survival relative to environmental events elucidates the linkage between oceanographic conditions and recruitment.

Temporal Patterns in Larval Survival

To evaluate the importance of seasonal changes in larval survival of the northern anchovy requires estimates of annual variation in recruitment. The age composition of the central population of northern anchovy is monitored through the fishery and trawl surveys. Mais (1981a) analyzed the age composition of the commercial fishery in southern California and suggested the following ranking of recent year classes: 1974 weak, 1975 weak, 1976 mediocre-strong, 1977 weak, and 1978 very strong. During the 1978-79 fishing season the 1978 year class of the northern anchovy contributed 65% of the southern California catch and in the following season the 1979 year class contributed 35% (Mais 1981a). In the spring 1979 trawl survey the 1978 year class contributed 62% and in spring 1980 the 1979 year class contributed 35% (Mais 1980, 1981b). Thus the fishery and the survey indicate that the 1978 year class was about twice as large as the 1979 year class.

This difference in recruitment cannot be explained by the abundance of young northern anchovy larvae. Northern anchovy larval production in 1979 was 2.1% greater than in 1978. Thus the larger 1978 year class resulted from higher survival because larval abundance was less in 1978 than in 1979.

The critical question is whether the recruitment variation described above requires more annual variation in larval survival than is caused by the seasonal changes described in this study. I evaluated this question by scaling the northern anchovy larval abundance estimates (Figs. 2, 3) with the ratio of larval abundance between the 2 years (0.979), and the monthly fractions of juvenile birth dates (Table 7) were scaled by the ratio of recruitments (2.0). The ratio, (scaled birth date fraction)/(scaled larval abundance fraction), estimates relative survival of a month's spawn (Fig. 4). Because of the scaling, these ratios can be compared both between and within years. Survival of winter spawn in 1979 was similar to survival of winter spawn in 1978, but survival was much greater in April-May 1978 than April-May 1979. Thus, the larger 1978 year class was not necessarily the result of greater survival throughout the spawning season. The increase in survival during the last 2 major months of the 1978 spawning season was sufficient to cause a large increase in recruitment.

Detection of Changes in Survival

Detection of a match between spawning and favorable environmental conditions of the northern anchovy seems more likely than detection of an event which results in poor survival. If a short-duration favorable environmental period results in a doubling of year class abundance, then more than half of the year class would have been born during that period. Such a concentration of birth dates could have been, but was not, detected in 1978 and 1979. A particular match apparently was not necessary for these two year classes. Conversely, a short-duration unfavorable environmental period that destroys all northern anchovy larvae born during the period may cause only a small reduction in year class abundance and a short gap in the birth-date distribution that would be difficult to detect with small sample sizes.

The effect of other environmental events will be more difficult to detect. Long-duration events or events that affect larvae of a wide age range will have little effect on the birth-date distribution. Secondly, environmental events which do not extend over the geographic range of spawning may not be detected even though they have important local effects.

Spatial Pattern

This study was designed to study temporal changes in frequency of juvenile birth dates but a strong spatial pattern also was detected. Northern anchovy juveniles collected north of Pt. Dume were larger than southern juveniles because of earlier birth dates. Hewitt and Methot (1982) showed that spawning contracted towards the San Diego area as the 1978 and 1979 spawning seasons progressed. This trend would contribute to an earlier mean birth date for northern fish, if currents and eddies did not substantially redistribute the larvae. In addition, if juveniles routinely move northward along the coast, early born fish will be further north by November. There are no data on the distribution of late larvae with which to investigate the cause of latitudinal pattern in juvenile birth dates. Geographic pattern in birth date will contribute to geographic pattern in size at age of adults.

Relation to Environmental Conditions

Two oceanographic factors, stability of the upper water column (Lasker 1978) and offshore transport (Parrish et al. 1981), have been suggested as factors in recruitment of northern anchovy. These factors should have had different effects on recruitment in 1978 and 1979.

Lasker (1975, 1978) suggested that northern anchovy larvae are likely to encounter adequate prey concentrations only when the upper water column is stable and prey are aggregated into layers. Of particular importance is the inshore chlorophyll maximum layer which may be composed of dinoflagellates suitable as prey for first feeding larvae. These layers are homogenized as storms or upwelling events destroy the stratification of the upper tens of meters of the water column. The winter of 1977-1978 was particularly stormy (Lasker 1981) and the isothermal surface layer was as deep as 50 m until stratification was restored in March. This hypothesis correctly predicts lower larval survival in winter 1978 than in spring 1978, but incorrectly predicts a poor year class in 1978.

Any hypothesis concerning the availability of prey will predict increasing survival through the major spawning season (December to June). Zooplankton biomass increases to its seasonal maximum in June (Smith and Lasker 1978). Stratification (differences between temperature at 10 and 30 m) increases so the prey of larval fish probably are increasingly aggregated into layers. Day length increases so that larvae can feed longer per day (Hunter 1972). A measurable response of northern anchovy larvae to the above factors is an increase in growth rate from 0.43 mm/d in January to 0.55 mm/d in June (Methot 1981) despite trivial changes in mean temperature (Table 3). If food availability is important to larval survival then survival should consistently increase through the spawning season.

The second major hypothesis concerns offshore transport and coastal upwelling caused by the predominantly northwest winds (Parrish et al. 1981).

Northern anchovy larvae which are transported offshore may experience higher larval mortality rates, and the survivors may be unable to return to the inshore juvenile nursery areas. Monthly indices of upwelling (Bakun 1973) at lat. 30° and 33°N, relative to long-term monthly means, were exceptionally low during January-March 1978 (downwelling occurred) and remained below normal through May 1978 (McLain and Ingraham 1980). Seckel et al. (1978) suggested that these conditions entrained larvae close to shore and correctly predicted an abundant 1978 year class. However, the results obtained here suggest that larval survival was higher during late spring 1978 than during the winter when downwelling occurred.

Upwelling was as low in December 1978 and January 1979 as in winter 1978, but the storms were less severe in 1979. Later in 1979, upwelling was near normal. The increased upwelling in 1979 relative to 1978 may have been responsible for the greater offshore displacement of northern anchovy larvae in 1979 (Table 4). The transport hypothesis correctly predicts a poorer year class in 1979 relative to 1978 and decreasing larval survival through the 1979 spawning season.

This brief examination of environmental data does not completely account for the patterns of recruitment of the northern anchovy in 1978 and 1979. Indices of offshore transport seem more important than indices of food availability, but the seasonal pattern of survival in 1978 could not be explained by transport. It is simplistic to assume that only one factor is involved in recruitment and that the effect of this factor is linear. One plausible scenario is that the winter storms of 1978 caused high mortality of early larvae, but the low upwelling throughout the year permitted high entrainment of late larvae and resulted in the good year class. It is also possible that the extremely low upwelling during winter 1978 did not have a proportionally greater effect than the low upwelling of spring 1978. Relatively low upwelling late in the spawning season may be important because absolute upwelling and transport typically increase through the spring (Smith and Lasker 1978). The spawning season may be timed to avoid low food availability in winter and high transport in late spring.

Other evidence indicates that survival of early northern anchovy larvae was nearly constant during the 1978 and 1979 spawning seasons. Hewitt and Methot (1982) inferred larval mortality from the slopes of the larval age-frequency distributions and found no significant seasonal changes. This evidence is consistent with the hypothesis that the significant change in survival which caused the difference in recruitment occurred after the early larval stage. Adverse larval drift would not necessarily cause increased mortality during the age interval examined by Hewitt and Methot but may affect the fraction of the surviving larvae which are entrained in the range of the juvenile habitat.

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HETEROCARPUS LONGIROSTRIS MacGILCHRIST FROM THE NORTHERN MARIANA ISLANDS

In March and April 1981 the National Marine Fisheries Service Honolulu Laboratory chartered the FV *Typhoon* to conduct a fisheries resource survey in the waters of the Commonwealth of the Northern Mariana Islands. One of the major objectives of this survey was the investigation of deepwater pandalid shrimp stocks. Although not previously recognized as a species of commercial interest (Holthuis 1980), *Heterocarpus longirostris* MacGilchrist 1905 was caught in sufficient numbers on this cruise to suggest a commercial potential.

Heterocarpus longirostris has been recorded in the literature from a few specimens caught in the Indian Ocean. MacGilchrist (1905) reported taking two male specimens at 1,754 m in the Bay of Bengal; Balss (1925), one female specimen taken at 1,143 m off Nias Island, Sumatra; and Calman (1939), one female specimen taken at 914-1,463 m in the Maldive area. Catches from this cruise constitute a first record of this species from the Pacific Ocean. *Heterocarpus longirostris* is very similar to *H. laevigatus* in general morphology. *Heterocarpus longirostris* differs from *H. laevigatus* in that the preorbital dorsal surface of the rostrum is multidentate and there is a blunt point posteriorly on the carina of the third abdominal somite. In *H. laevigatus* the dorsal surface of the rostrum is edentate in advance of the orbit and the posterior portion of the third abdominal somite is rounded. Further differences are discussed in MacGilchrist (1905).

The FV *Typhoon* fished for shrimp in the Saipan-Tinian area using traps baited with chopped fish, usually skipjack tuna, *Katsuwonus pelamis*. The traps consisted of half-round frames of iron rebar (91 × 72 × 42 cm) wrapped with 13 × 25 mm or 13 × 13 mm wire mesh and covered by either burlap or canvas over the arched upper surface. On each sampling day one string of three traps was set at each of three sampling depths, 366, 732, and 1,097 m (200, 400, and 600 fathoms). Strings were set in the afternoon and recovered the next morning with a normal soaking time of between 16 and 20 h. Three species of *Heterocarpus*—*H. ensifer, H. laevigatus,* and *H. longirostris*—accounted for the majority of the catch. Shrimp referable to both *H. laevigatus* and *H. longirostris* were present in the catches throughout the cruise, but during the major part of the cruise they were considered to be the same species and recorded as "*H. laevigatus.*" These two species were recorded separately only on the last two series of sets (two strings at each of the three experimental depths). Information on the catch for these six strings is presented in Table 1.

The species with the highest catch rate (kilograms per trap) was *H. laevigatus; H. ensifer* and *H. longirostris* followed with catch rates about half that of *H. laevigatus. Heterocarpus laevigatus* was also the largest species caught, averaging 25 individuals/kg. *Heterocarpus longirostris* was next, averaging 47/kg, and *H. ensifer* was the smallest, averaging 146/kg. Differences in the reproductive biology of these species are suggested by the differing proportion of egg-bearing females present in the catch for each species. The percentage of berried females was highest for *H. ensifer* at 33% whereas that for *H. longirostris* was only 19%, and no berried *H. laevigatus* were caught. It is quite likely that these values change on a seasonal basis. Vertical separation of the three species was complete for the last six strings set. *Heterocarpus ensifer* was caught only at 366 m, *H. laevigatus* only at 737 m, and *H. longirostris* only at 1,097 m.

Though not documented due to confusion in the species identification of *H. laevigatus* and *H. longirostris* during most of the cruise, there is reason to believe that species separation by depth was essentially complete for the entire cruise. Table 2 lists the catch of the three species of *Heterocarpus* for the entire cruise excluding the last six strings. *Heterocarpus ensifer* was found almost exclusively at 366 m with a few being caught at 732 m. Mean size and percentage of berried female values for the entire cruise (Table 2) are very similar to those obtained from the last six strings (Table 1) for *H. ensifer* (112/kg compared with 146/kg and 31% compared with 33%, respectively). Similarly, values of mean size and percent berried for *H. laevigatus* in Table 1 match closely those for the *H. laevigatus/H. longirostris* group at 732 m (and the few at 366 m) in Table 2 as do the values for *H. longirostris* (Table 1) with those at 1,097 m (Table 2). This supports the assumption of vertical separation of these three species.

Both *H. laevigatus* and *H. ensifer* are considered to be commercially important species and have supported small local fisheries in some Pacific areas (Hawaii State 1979). Based on the results of this cruise, *H. longirostris* compares favorably with these two species as one with commercial potential. It is very close to *H. ensifer* in relative abundance (mean catch in weight per trap) and second, to *H. laevigatus*, in mean size. *Heterocarpus laevigatus* is first in both

TABLE 1.—Catch of *Heterocarpus ensifer, H. laevigatus,* and *H. longirostris* for the last six strings of the cruise.

Depth (m)	No. of traps fished	Catch			Mean catch/ trap (kg)	Mean size of shrimp (No./kg)	Percent berried
		Species	Number	Weight (kg)			
366	6	*H. ensifer*	542	3.7	0.6	146	33
732	6	*H. laevigatus*	172	7.0	1.2	25	0
1,097	6	*H. longirostris*	170	3.6	0.6	47	19

TABLE 2.—Catch of *Heterocarpus ensifer, H. laevigatus,* and *H. longirostris* for the entire cruise excluding the last six strings.

Depth (m)	No. of traps fished	Catch			Mean catch/ trap (kg)	Mean size of shrimp (No./kg)	Percent berried
		Species	Number	Weight (kg)			
366	34	*H. ensifer*	1,580	14.05	0.4	112	31
366	34	*H. laevigatus/H. longirostris*	67	3.5	0.1	19	1.5
732	56	*H. ensifer*	35	0.3	0.01	117	17
732	56	*H. laevigatus/H. longirostris*	2,654	90.75	1.6	29	1.6
1,097	57	*H. laevigatus/H. longirostris*	1,920	35.9	0.6	53	21

categories. Although further survey work is needed to determine the depth of maximum abundance for *H. longirostris,* the apparent greater depth of habitat for this species (1,097 m as compared with 766 m for *H. laevigatus* and 366 m for *H. ensifer)* is the major undesirable characteristic for development of any proposed fishery. Fishing at these greater depths would require greater capital investment not only in a more powerful depth recorder but also in expensive line which would need to be replaced after any gear loss.

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ROBERT B. MOFFITT

Southwest Fisheries Center Honolulu Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 3830
Honolulu, HI 96812

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DESCRIPTION OF EARLY STAGES OF WHITE SEABASS, *ATRACTOSCION NOBILIS*, WITH NOTES ON DISTRIBUTION

H. GEOFFREY MOSER, DAVID A. AMBROSE, MORGAN S. BUSBY, JOHN L. BUTLER, ELAINE M. SANDKNOP,
BARBARA Y. SUMIDA, AND ELIZABETH G. STEVENS
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038

ABSTRACT

Eggs, larvae, and juveniles of *Atractoscion nobilis*, reared in the laboratory, are described and compared with those of *Cynoscion* species. Eggs of *A. nobilis* are among the largest reported for a sciaenid species (1.24-1.32 mm diameter), and the larvae have a distinctive morphology and pigment pattern that contrasts sharply with that of *Cynoscion* species. The larvae are robust, with long pectoral and pelvic fins and have a solid pigment sheath of melanophores and xanthophores that initially covers the head and trunk and expands to cover the body completely. The only other sciaenid with similar developmental stages is *Sciaena umbra* of the eastern Atlantic, Mediterranean, and Black Sea. Late-stage larvae of *Larimus fasciatus* of the western Atlantic have large, heavily pigmented paired fins, but the body pigment is not a solid cloak as in *A. nobilis*.

Atractoscion larvae occurred in only 104 samples of all CalCOFI collections made between 1950 and 1978. Larvae occurred from Santa Rosa Island, California, to Santa Maria Bay, Baja California, with highest concentrations in the Sebastian Viscaino Bay and San Juanico Bay regions. Most of the larvae occurred from May to August, with a peak in July.

RESUMEN

Se describen los huevos, larvas y juveniles de *Atractoscion nobilis* cultivadas en el laboratorio, y se comparan con especies de *Cynoscion*. Entre las especies de Sciaenidae, los huevos con mayores dimensiones corresponden a *A. nobilis* (1.24-1.32 mm. de diámetro), y sus larvas muestran una morfología bien definida, con el pigmento distribuido de forma diferente a la que presentan las especies de *Cynoscion*. Las larvas son robustas, con aletas pectorales y pélvicas largas, y llevan pigmento que incluye melanoforos y xantoforos. Esta capa de pigmento cubre inicialmente la cabeza y tronco, extendiéndose hasta cubrir completamente el cuerpo. *Sciaena umbra* es otro Sciaenidae con fases de desarrollo similar, y habita el Atlántico oriental, Mar Mediterráneo y Mar Negro. Las últimas fases larvales de *Larimus fasciatus* del Atlántico occidental, son de gran tamaño, con aletas pares densamente pigmentadas, pero la pigmentación del cuerpo no es una capa continua como en *A. nobilis*.

De todas las colecciones de CalCOFI efectuadas entre 1950 y 1978, únicamente 104 muestras contenían larvas de *Atractoscion*. Estas larvas se distribuían desde la Isla Santa Rosa, California, hasta Bahía Santa María, Baja California (México), y las mayores concentraciones de larvas aparecían en las zonas de las Bahías Sebastián Vizcaíno y San Juanico. La mayor parte de las larvas se obtuvieron en el período de Mayo hasta Agosto, con máximos en Julio.

INTRODUCTION

The white seabass, *Atractoscion nobilis*, is the largest sciaenid inhabiting the waters off California and western Baja California and, because of its size and high food quality, has been a prized sport and commercial species. Vojkovich and Reed (1983) summarize the decline of the fishery, despite numerous management regulations imposed since 1931, and emphasize the need for information about early life history.

The taxonomic status of the white seabass has been unclear since the original description of Ayres (1860), who placed it in the genus *Johnius*. Gill (1863) established the genus *Atractoscion* to include *A. aequidens* of the southern African and Australian coasts, and the white seabass. Jordan and Evermann (1898) made *Atractoscion* a subgenus of *Cynoscion*, and Trewavas (1977) re-established the genus *Atractoscion* to include *A. aequidens* and *A. nobilis*, based primarily on the fact that these two species lack the adult canine teeth typical of other *Cynoscion* species.

The purpose of this paper is to describe the early life history of *A. nobilis* and to present data on seasonal distribution of larvae from CalCOFI collections. Also, the early stages of *A. nobilis* are compared with those of *Cynoscion* to provide additional taxonomic characters of cynoscionine fishes.

MATERIALS AND METHODS

Specimens used in the description came from four sources. The original identification was based on a

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single larva taken from a reared batch of sciaenid eggs, mostly *Cheilotrema saturnum*, collected by plankton net at the surface off Tourmaline Canyon, San Diego, on July 6, 1978. The 8.3-mm larva was sampled on July 31, 25 days after collection. Temperature range of the 100-l rearing tank was 18.7-21.7°C, and the larva was fed a diet of the rotifer *Brachionus plicatilis* and nauplii of *Artemia salina*. A second source of specimens was a batch of eggs provided by the aquarium at Scripps Institution of Oceanography. On June 13, 1980, the eggs appeared in a tank containing two white seabass that had been collected as one-year-old fish and maintained in the tank for two years. The eggs were transported to the Southwest Fisheries Center and placed in a 100-l rearing tank. Hatching occurred after 3 days, and yolk was exhausted on about day 6, at which time *B. plicatilis* was added to the tank. The larvae did not feed, and all were dead on day 10. Temperature range in the tank was 16.5-20.0°C.

The principal sources of larvae were from two spawnings of captive adult *A. nobilis* maintained under modified environmental conditions at the Southwest Fisheries Center by Roger Leong (pers. comm.). The first spawning was on March 18, 1982, and, for a period of 8 days, specimens were supplied to us by Carol Kimbrell. The second spawning was on April 12, 1982, and larvae were reared by Carol Kimbrell according to procedures described in Hunter and Kimbrell (1980). Specimens were supplied to us daily, and some were photographed, after anesthetization in MS-222, to record live color pattern. All specimens were preserved in 4% Formalin.

One series was assembled to describe changes in morphology and pigment pattern, and another to describe head-spine formation and ossification of meristic elements. For comparative purposes, two series of *Cynoscion acoupa maracaiboensis* were also assembled from specimens supplied by Dr. Raymond Olivares, University del Zulia, Maracaibo, Venezuela. Techniques and terms used in the description follow those outlined in Moser and Ahlstrom (1970, 1978) and Ahlstrom et al. (1976).

Distributional data were obtained by examining all ichthyoplankton samples containing sciaenids taken by CalCOFI from 1950 to 1978, and by identifying and measuring specimens of *A. nobilis*.

DESCRIPTION (Figures 1-4)

Distinguishing Features

Eggs are larger (1.24-1.32 mm diameter) and have a larger oil globule (0.30-0.36 mm diameter) than those of the six other sciaenid species off California (Watson 1982, *Genyonemus lineatus;* Moser et al., other species[1]). Egg diameter of the other sciaenids is less than 1.0 mm, and oil globule diameter is less than 0.26 mm. Larvae hatch at a larger size (ca. 2.8 mm) and are larger at yolk depletion (3.7 mm) than in the other species, which hatch at 1.4-1.8 mm and are 2.4-3.0 mm at yolk depletion. First-feeding larvae are distinguished by a melanistic sheath that covers the head and trunk to slightly posteriad of the anus. *Menticirrhus undulatus* is similar but less intensely pigmented, is less robust, and is smaller at comparative states of development. Beyond initial feeding stages *A. nobilis* larvae become deep-bodied, and develop a large broad head and a solid pigment cloak that gradually covers the entire body. After notochord flexion the paired fins become enlarged and heavily pigmented, and a characteristic banding pattern develops on the body.

Eggs

The eggs of *A. nobilis* are among the largest known for Sciaenidae. For 25 eggs measured from the June 13, 1980, spawning the diameter range was 1.24-1.32 mm ($\bar{x}$ = 1.27 ± 0.02 SD), with an oil globule diameter range of 0.30-0.36 mm ($\bar{x}$ = 0.33 ± 0.02 SD). In the developing embryo the oil globule is located posteriad in the yolk sac. Melanophores begin to appear on the embryonic axis within the first day, and the embryo develops a solid sheath of melanophores on the head and trunk before hatching. Melanophores on the oil globule are concentrated on the inner surface.

Morphology

At hatching the larva is relatively undifferentiated and has a large ovoid yolk sac (ca. 0.9 × 1.5 mm). During the yolk-sac period relative snout-anus length and overall body depth decrease as the yolk is depleted (Table 1), and at the termination of the yolk-sac stage the gut begins to coil. The pectoral fin buds appear about midway through the yolk-sac period and have a well-differentiated base and blade by the end of the period.

During the preflexion and flexion stages relative snout-anus length, head length, head width, snout length, and body depth increase while relative eye diameter decreases gradually (Tables 1, 2). At notochord flexion, larvae have attained their highly characteristic morph—a massive head with large jaws, a pronounced convex dorsal profile, and a deep, robust trunk region that tapers gradually to a narrow caudal peduncle. In postflexion larvae there is a con-

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[1] Manuscript (in preparation) on early stages of sciaenid species off California

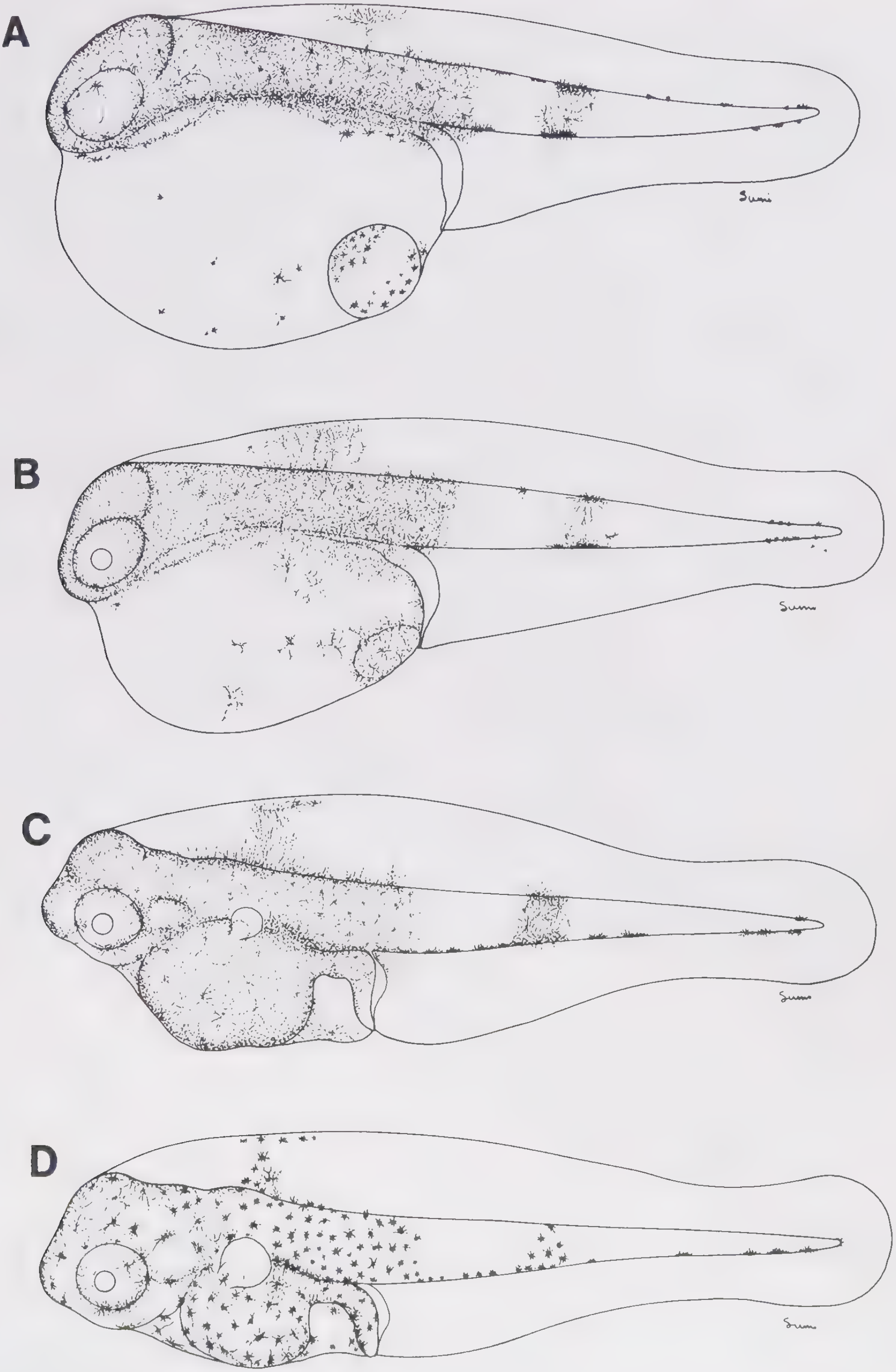

Figure 1. Yolk-sac larvae of *Atractoscion nobilis* from July 13, 1980, spawning. *A*. 2.8 mm, day 3; *B*. 3.2 mm, day 3; *C*. 3.5 mm, day 4; *D*. 3.7 mm, day 5

TABLE 1
Measurements (mm) of Early Stages of *Atractoscion nobilis*

Body length	Age (days)	Snout-anus distance	Head length	Head width	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Yolk sac length	Yolk sac depth	Oil globule diameter
2.8	3	1.6	0.76	0.42	0.10	0.27	1.1	—	—	—	1.5	0.90	0.36
3.2	3	1.7	0.70	0.47	0.15	0.30	0.94	—	—	—	1.3	0.86	0.36
3.5	4	1.6	0.75	0.46	0.13	0.32	0.81	—	0.15	—	0.81	0.57	0.35
3.7	5	1.6	0.78	0.55	0.18	0.34	0.71	—	0.27	—	0.57	0.50	0.26
3.5	7	1.6	0.91	0.65	0.17	0.32	0.81	0.19	0.30	—	—	—	0.15
3.7	7	1.7	0.90	0.74	0.16	0.37	0.96	0.22	0.31	—			
4.0	8	1.8	1.0	0.79	0.22	0.40	1.0	0.25	0.35	—			
4.2	10	1.9	1.2	0.81	0.28	0.41	1.0	0.26	0.42	—			
4.5	10	2.1	1.2	0.88	0.25	0.44	1.2	0.28	0.44	—			
4.7	10	2.3	1.3	0.90	0.28	0.48	1.3	0.29	0.48	—			
5.1	14	2.4	1.4	1.0	0.35	0.49	1.5	0.29	0.52	—			
5.2	15	2.6	1.3	1.0	0.3	0.53	1.5	0.35	0.52	0.08			
5.5	15	2.6	1.5	1.2	0.38	0.55	1.7	0.36	0.60	0.08			
5.7	15	2.8	1.7	1.2	0.50	0.62	1.8	0.40	0.62	0.11			
5.9	15	2.9	1.7	1.2	0.50	0.64	1.9	0.46	0.60	0.10			
6.0	18	2.9	1.8	1.4	0.51	0.67	2.0	0.52	0.62	0.13			
6.2	18	3.1	2.0	1.5	0.48	0.68	2.1	0.46	0.65	0.20			
6.5	22	3.5	2.0	1.5	0.54	0.67	2.2	0.63	0.75	0.33			
6.8	22	4.0	2.3	1.6	0.50	0.83	2.6	0.80	0.76	0.49			
7.0	25	4.0	2.4	1.7	0.58	0.84	2.6	1.0	0.75	0.72			
7.4	25	4.2	2.6	1.9	0.66	0.89	2.8	1.2	0.81	0.88			
7.8	25	4.6	2.8	1.8	0.64	0.88	2.8	1.2	0.78	0.85			
8.2	25	5.1	3.0	1.9	0.62	0.94	2.9	1.4	0.80	1.0			
8.8	30	5.4	3.1	2.1	0.86	1.0	3.6	1.9	0.84	1.5			
9.2	30	5.6	3.2	2.4	0.95	1.0	3.5	1.8	0.83	1.7			
9.6	30	6.1	3.3	2.6	0.90	1.1	3.8	2.1	1.0	1.8			
10.0	29	6.4	3.4	2.5	0.92	1.0	3.6	2.0	0.84	1.7			
10.5	37	7.2	3.8	2.5	1.1	1.2	3.9	2.6	0.92	—			
10.7	37	7.2	4.0	2.6	1.0	1.2	3.8	3.0	1.0	2.0			
11.3	37	7.1	4.2	2.6	1.1	1.3	4.1	3.0	1.0	2.4			
11.7	37	7.8	4.2	2.7	1.1	1.3	4.2	2.9	1.0	2.3			
12.0	37	7.8	4.4	2.9	1.2	1.3	4.4	3.0	0.94	2.5			
12.2	37	7.8	4.3	2.9	1.2	1.3	4.2	3.3	1.0	2.7			
12.8	44	8.3	4.5	3.0	1.2	1.4	4.5	3.5	1.0	2.7			
13.1	36	9.2	5.0	2.9	1.2	1.5	4.8	3.6	1.0	2.9			
13.9	36	9.3	5.1	3.0	1.2	1.5	4.8	3.7	1.1	2.9			
14.9	44	10.3	5.2	3.5	1.3	1.7	5.2	4.2	1.1	3.6			
15.5	52	10.8	5.6	3.3	1.5	1.8	5.2	3.8	1.1	3.3			
15.8	48	11.3	6.3	3.3	1.9	1.5	4.9	4.2	1.1	3.7			
17.1	44	11.7	5.8	3.8	1.8	1.5	6.1	4.8	1.2	3.8			
17.2	49	11.8	7.2	3.4	1.5	1.9	6.3	5.3	1.1	4.3			
17.7	42	12.2	6.2	3.4	1.6	1.9	5.5	4.5	1.2	3.8			
18.7	48	13.3	7.5	4.0	1.9	2.1	6.3	5.3	1.2	3.8			
20.2	46	13.8	7.5	4.2	1.4	1.8	6.8	5.5	1.3	5.2			
20.5	46	14.2	7.3	4.2	1.6	2.0	6.7	5.6	1.3	4.8			
22.8	46	16.2	8.5	5.0	1.9	2.3	7.5	5.8	1.3	5.3			
23.0	46	16.2	7.8	4.5	2.0	2.2	7.6	6.0	1.4	5.3			
27.3	57	19.3	8.8	5.0	1.9	2.5	8.8	6.7	1.6	6.2			
38.1	76	26.6	13.8	6.0	2.7	3.5	10.7	8.0	1.9	6.3			
38.4	76	26.3	13.0	5.4	2.7	3.3	10.8	—	2.0	6.3			
53.6		37.1	17.2	7.2	4.2	3.7	14.0	9.7	2.5	10.0			
64.7		45.1	20.3	8.8	5.0	4.3	17.0	11.3	2.5	11.7			
75.2		51.9	22.8	10.0	5.3	5.2	20.2	12.7	3.2	13.3			
82.0		57.3	24.6	9.5	7.0	5.3	22.2	—	3.4	13.6			
98.4		69.5	30.3	13.0	6.7	5.8	24.7	—	4.2	15.3			

Specimens between dashed lines are undergoing notochord flexion. Specimens between solid lines are reared juveniles. Specimens below solid line are juveniles from Scripps Institution of Oceanography fish collection.

tinued relative increase in snout-anus length. Relative head length and body depth are slightly greater than in the previous stage. Relative snout length remains constant, but relative head width and eye diameter continue to decrease slightly. There is a gradual deepening of the body during this stage, to become somewhat slab-sided, and the entire dorsal profile becomes strongly arched, tapering abruptly at the caudal pedun-

TABLE 2
Morphometry of Larvae and Early Juveniles of *Atractoscion nobilis*

	Snout-anus distance / Body length	Head length / Body length	Head width / Head length	Snout length / Head length	Eye diameter / Head length	Body depth / Body length	Pectoral fin length / Body length	Pectoral base depth / Body length	Pelvic fin length / Body length
Preflexion									
$\bar{x}$ ± SD	47.6 ± 4.06	25.1 ± 2.69	69.9 ± 7.43	20.2 ± 3.26	38.5 ± 3.58	26.6 ± 5.18	6.0 ± 0.33	8.6 ± 1.90	—
(range)	(43.2 – 57.1)	(21.1 – 28.6)	(55.3 – 82.2)	(13.2 – 25.0)	(34.2 – 43.6)	(19.2 – 39.3)	(5.4 – 6.3)	(4.3 – 10.2)	—
N	11	11	11	11	11	11	7	9	0
Flexion									
$\bar{x}$ ± SD	50.8 ± 3.75	29.7 ± 2.77	74.4 ± 3.81	26.0 ± 2.95	36.0 ± 2.86	32.8 ± 2.75	8.2 ± 1.81	10.8 ± 0.61	3.0 ± 2.07
(range)	(47.3 – 58.8)	(25.0 – 33.8)	(69.6 – 80.0)	(21.7 – 29.4)	(31.6 – 40.8)	(28.8 – 38.2)	(6.5 – 11.8)	(10.0 – 11.6)	(1.5 – 7.2)
N	8	8	8	8	8	8	8	8	8
Postflexion									
$\bar{x}$ ± SD	64.2 ± 4.02	35.8 ± 1.15	66.7 ± 5.63	25.9 ± 2.21	31.4 ± 1.58	36.4 ± 1.80	23.0 ± 4.61	8.8 ± 1.14	18.3 ± 4.23
(range)	(56.8 – 70.2)	(24.0 – 38.2)	(58.0 – 78.8)	(20.7 – 29.7)	(29.4 – 35.0)	(33.5 – 40.9)	(14.3 – 28.2)	(7.1 – 10.9)	(10.3 – 24.2)
N	19	19	19	19	19	19	19	19	18
Reared Juveniles									
$\bar{x}$ ± SD	69.7 ± 1.20	36.8 ± 2.65	53.4 ± 6.73	22.6 ± 2.57	27.6 ± 2.18	32.4 ± 2.58	26.4 ± 2.49	23.5 ± 1.90	22.2 ± 3.11
(range)	(68.3 – 71.5)	(33.9 – 41.9)	(41.5 – 65.5)	(18.7 – 25.9)	(24.0 – 31.0)	(28.1 – 36.6)	(21.0 – 28.3)	(20.8 – 26.7)	(16.4 – 25.7)
N	12	12	12	12	12	12	11	11	11
Field-Collected Juveniles									
$\bar{x}$ ± SD	69.7 ± 0.63	30.9 ± 0.85	42.1 ± 2.10	24.6 ± 2.42	21.2 ± 1.34	26.3 ± 0.79	17.5 ± 0.60	24.4 ± 1.99	17.3 ± 1.27
(range)	(69.0 – 7.06)	(30.0 – 32.1)	(38.6 – 43.9)	(2.21 – 28.5)	(19.1 – 22.8)	(25.1 – 27.1)	(16.9 – 18.1)	(22.1 – 25.8)	(15.5 – 18.7)
N	5	5	5	5	5	5	3	3	5

Values given for each body part are expressed as percentage of body length or head length

cle. In reared juveniles relative head width and body depth decrease as the body becomes terete.

Fin Formation/Meristics

Ossification of the principal caudal fin rays begins at the initiation of notochord flexion (ca. 5.6 mm); however, the full complements of 9 + 8 principal and 8 + 7 procurrent rays have not begun ossifying until larvae reach about 7.1 and 14.5 mm, respectively (Table 3). Notochord flexion is complete at about 7.0 mm SL. Ossification of rays begins in the other fins about midway through notochord flexion. The full complement of IX-X + I, 19-23 dorsal rays is ossifying just after notochord flexion is complete. Anal fin formation is similar, with the soft rays ossifying first and the full count of I-II, 8-10 present just after flexion. Both fins become lobate in postflexion larvae and early juveniles, as does the caudal fin.

Ossification of rays in the paired fins begins at about 6.0 mm, midway through notochord flexion (Table 3). The full complements of 15-18 pectoral and I,5 pelvic rays are present in early postflexion larvae. The fins enlarge rapidly in the postflexion stage. Average relative pectoral fin length is three times

TABLE 3
Meristics from Cleared and Stained Larvae of *Atractoscion nobilis**

Day	Body length	Dorsal fin rays	Anal fin rays	Pectoral fin rays	Principal caudal fin rays	Procurrent caudal fin rays	Vertebrae	Branchiostegal rays	Pelvic rays
10	4.5	—	—	—	—	—	—	2	—
14	5.0	—	—	—	—	—	3	6	—
15	5.6	—	—	3	4 + 4	—	8	7	—
18	5.8	—	—	6	6 + 6	—	16	7	—
22	6.1	VIII + I,12	—,2	6	7 + 7	—	19	7	—,3
22	6.7	VIII + I,15	—,6	7	8 + 7	—	21	7	I,3
24	7.1	IX + I,18	I,8	12	9 + 8	0 + 1	20	7	I,5
25	7.6	IX + I,20	I,9	13	9 + 8	1 + 1	25	7	I,5
27	9.4	IX + I,22	II,10	16	9 + 8	4 + 4	25	7	I,5
37	9.9	X + I,22	II,10	18	9 + 8	6 + 6	25	7	I,5
35	11.0	X + I,21	II,9	17	9 + 8	7 + 7	25	7	I,5
42	13.5	X + I,19	II,10	17	9 + 8	7 + 7	25	7	I,5
42	14.5	X + I,23	II,10	17	9 + 8	8 + 7	25	7	I,5

*Counts of paired structures taken on left side.

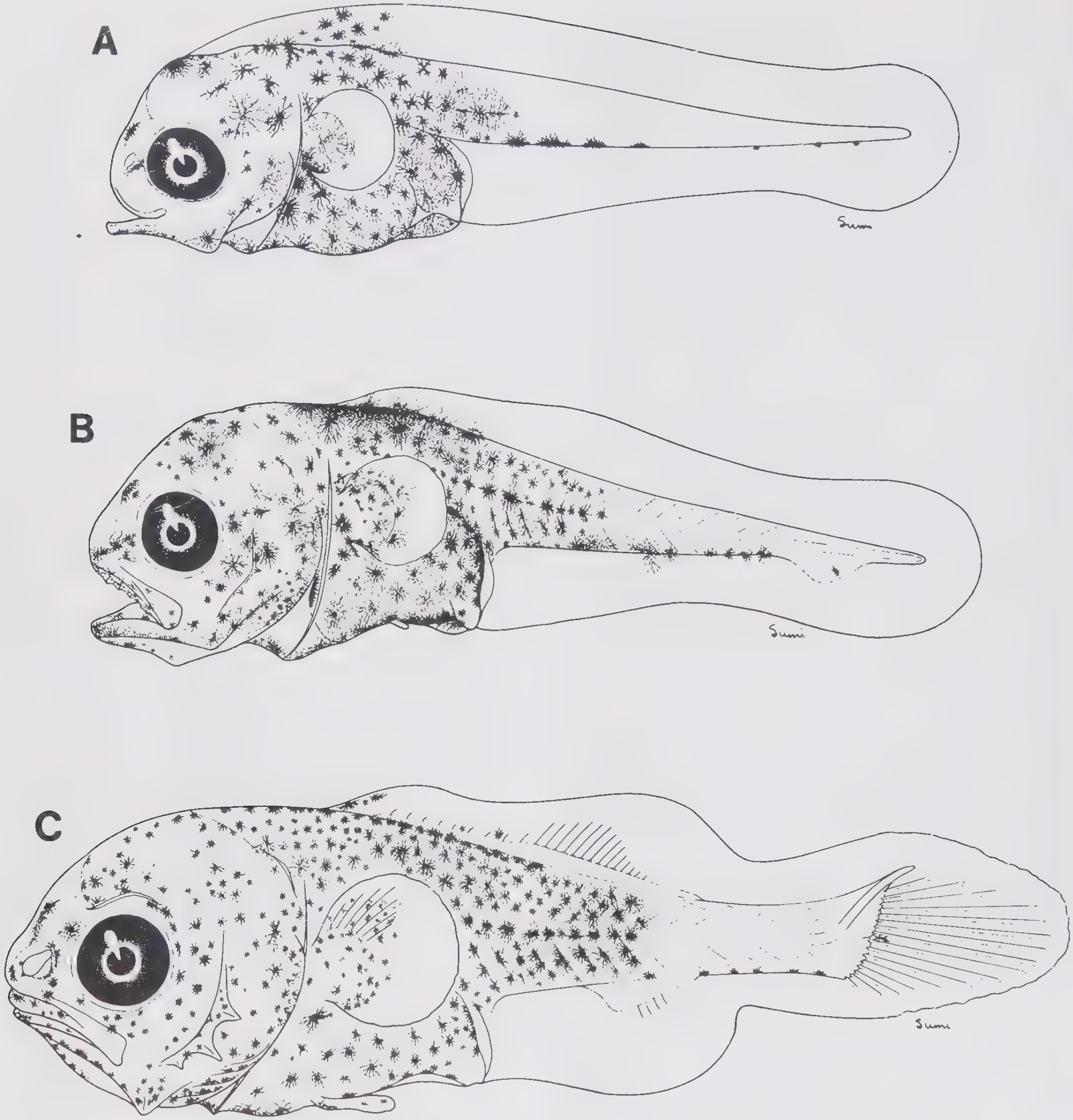

Figure 2. Larvae of *Atractoscion nobilis* from April 12, 1982, spawning. *A.* 3.7 mm, day 8; *B.* 5.1 mm, day 14; *C.* 6.5 mm, day 22.

greater in postflexion larvae than in flexion larvae, and relative pelvic fin length is six times greater. Both fins become lobate to somewhat fan-shaped in postflexion larvae (Figure 3).

Larvae begin to develop an array of head spines just before notochord flexion. The spines of the opercular series of bones appear first, with the preopercle developing the greatest number of spines (Table 4, Figures 3, 4). The posttemporal spines also develop early; the bone becomes trough-shaped, with spines forming on the anterior and posterior upturned edges. Anterior to the posttemporal bone, two scale bones develop in the region of the epiotic, one directly dorsal to the other. They too are trough-shaped and develop spines on the upturned edges. The frontal bone develops a supraocular crest bearing a series of spines. A longitu-

TABLE 4
Development of Head Spines (Left Side) in Larvae of *Atractoscion nobilis*

Bone	Location	Number of spines												
		Day												
		10	14	15	18	22	22	24	25	27	37	35	42	42
		Body Length (mm)												
		4.5	5.0	5.6	5.8	6.1	6.7	7.1	7.6	9.4	9.9	11.0	13.5	14.5
Preopercle	Anterior series	1	2	2	3	4	5	6	5	4	5	15	14	11
	Posterior series	—	2	3	3	3	4	5	5	6	10	8	12	8
Opercle		—	—	1	1	1	1	1	1	2	2	2	2	2
Subopercle		—	—	—	2	1	2	2	2	2	2	3	1	2
Interopercle		—	—	—	1	1	1	1	1	3	4	4	7	4
Posttemporal		—	—	—	—	—	—	—	1	6	10	7	7	6
Frontal	Supraocular	—	—	—	—	—	—	—	—	6	8	3	2	3
Pterotic		—	—	—	—	—	—	—	—	1	4	3	1	4
Scale Bone	Dorsal epiotic region	—	—	—	—	—	—	—	—	1	3	2	2	2
Scale Bone	Ventral epiotic region	—	—	—	—	—	—	—	—	1	4	4	3	3
Lacrymal		—	—	—	—	—	—	—	—	3	4	4	3	—
Dermospherotic		—	—	—	—	—	—	—	—	—	2	2	2	2
Circumorbitals		—	—	—	—	—	—	—	—	—	—	—	+	+

dinal crest develops on the pterotic, and bears up to 4 spines. The lacrymal bone develops 3-4 spines on its ventral margin at about 9.0 mm SL and, soon after, a small trough-shaped dermosphenotic (6th circumorbital) bone with 2 spines develops at the dorso-posterior margin of the orbit. At the end of the larval period 4 other circumorbitals develop around the posterior margin of the orbit, and each develops several spines.

Beginning at about 9.0 mm SL, scales, each with a single spine, appear on the opercle. They increase in number to almost cover the opercle at the end of the larval period.

Pigmentation

White seabass larvae develop two distinctive forms of pigmentation within a single pattern. Both melanophores and xanthophores begin to appear with equal prominence in the embryo; they increase in number and overlay each other almost exactly, to form a bicolored pattern. The following description applies to both melanophores and xanthophores, except as noted.

At hatching the entire head and trunk are pigmented solidly to slightly posteriad of the yolk mass (Figure 1). A postanal band is present on the tail, and, rearward of this, the dorsal and ventral midlines of the tail have melanophores only. This is the only place where both types of pigment cells are not present together. Above the trunk a tuft of pigment extends upward into the finfold and expands at the finfold margin. The oil globule is covered with pigment cells, and pigment is scattered over the yolk. As the yolk sac is depleted the gut mass becomes solidly pigmented, as does the pectoral fin base and, of course, the eye. At the end of the

TABLE 5
Measurements (mm) of Postflexion Larvae of *Cynoscion acoupa maracaiboensis*

Body length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length
7.3	4.2	2.4	0.6	0.56	2.2	—	—	0.16
7.6	4.3	2.8	0.6	0.64	2.5	0.80	0.40	0.72
7.8	4.4	2.7	0.6	0.64	2.7	0.88	0.44	0.68
8.1	4.8	2.9	0.7	0.70	2.7	0.92	0.52	0.76
8.9	5.6	3.3	0.8	0.80	2.9	1.2	0.64	0.88
9.3	6.2	3.4	0.9	0.72	2.8	0.80	0.64	0.72
10.3	6.9	3.7	1.0	0.80	3.2	1.5	0.80	1.1
10.5	7.0	4.1	0.96	1.0	3.2	1.84	0.64	1.2
13.5	9.4	5.3	1.3	1.1	4.2	—	0.76	2.1
14.2	9.5	5.2	1.1	1.3	4.4	3.1	0.84	2.1
$\bar{x}$ ± SD	6.29 ± 5.10	36.3 ± 2.09	8.8 ± 0.81	23.2 ± 1.56	31.8 ± 1.51	12.4 ± 4.56	6.1 ± 1.12	10.0 ± 3.74
(range)	(56.4 – 69.8)	(32.3 – 39.5)	(7.6 – 9.9)	(20.3 – 24.8)	(29.6 – 34.4)	(6.0 – 21.7)	(3.8 – 7.8)	(2.2 – 15.4)
N	10	10	10	10	10	10	10	10

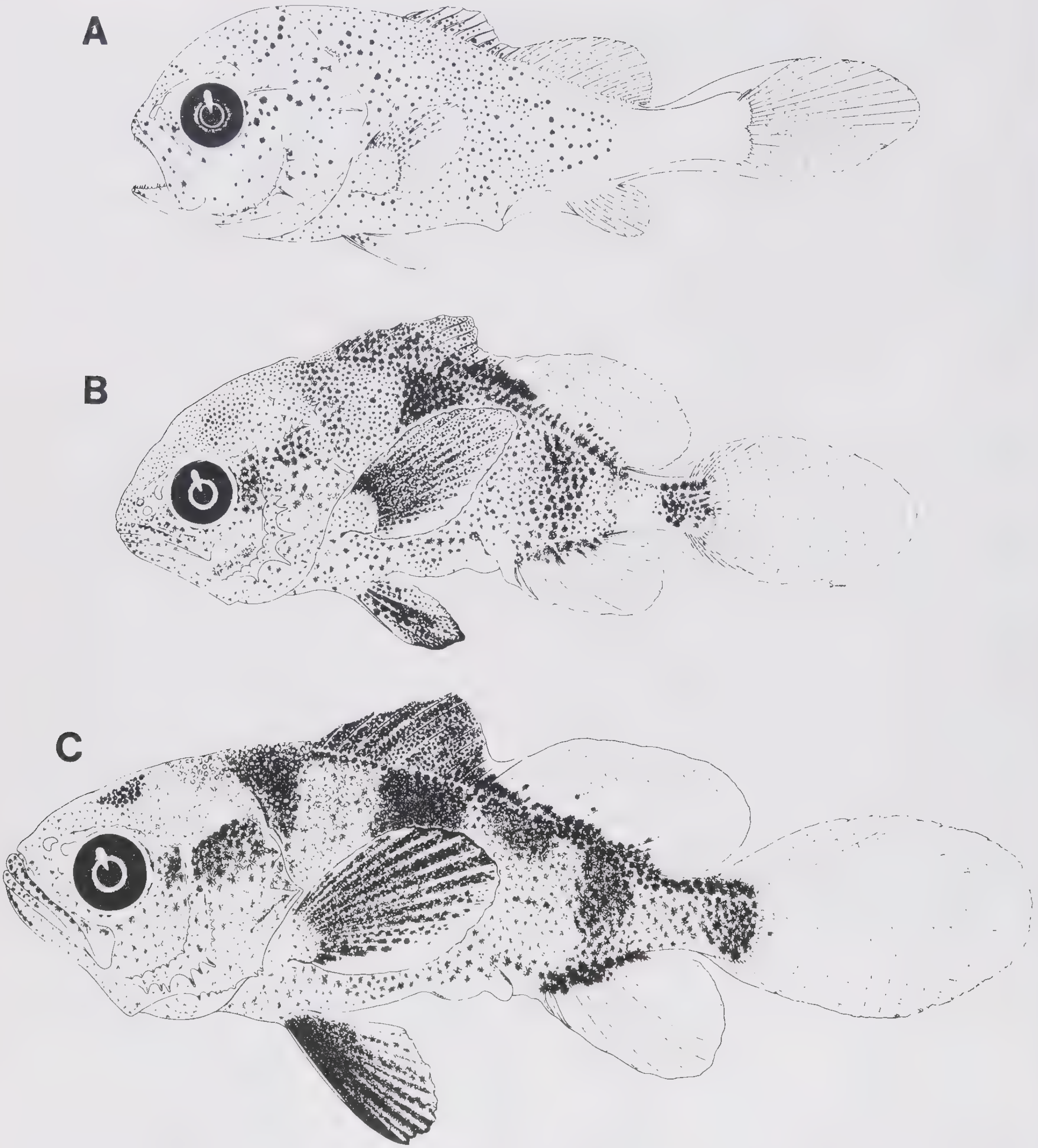

Figure 3. Larvae of *Atractoscion nobilis*. *A*. 8.3 mm, specimen reared from planktonic egg collection July 6, 1978, day 25. Note contracted state of melanophores; *B*. 10.7 mm, from April 12, 1982, spawning, day 37; *C*. 14.9 mm, from April 12, 1982, spawning, day 44.

yolk-sac period a postanal band is still present, but the dorsal midline melanophores are absent.

At the end of the first week (ca. 3.7 mm) the postanal band disappears. The postanal ventral midline series remains, with the melanophores of the anterior half of the series larger than those of the posterior half. The melanophores of the body cloak lying over the horizontal septum posterior to the pectoral fin appear larger and stand out as a line. Pigment begins to form on the pectoral fin blades.

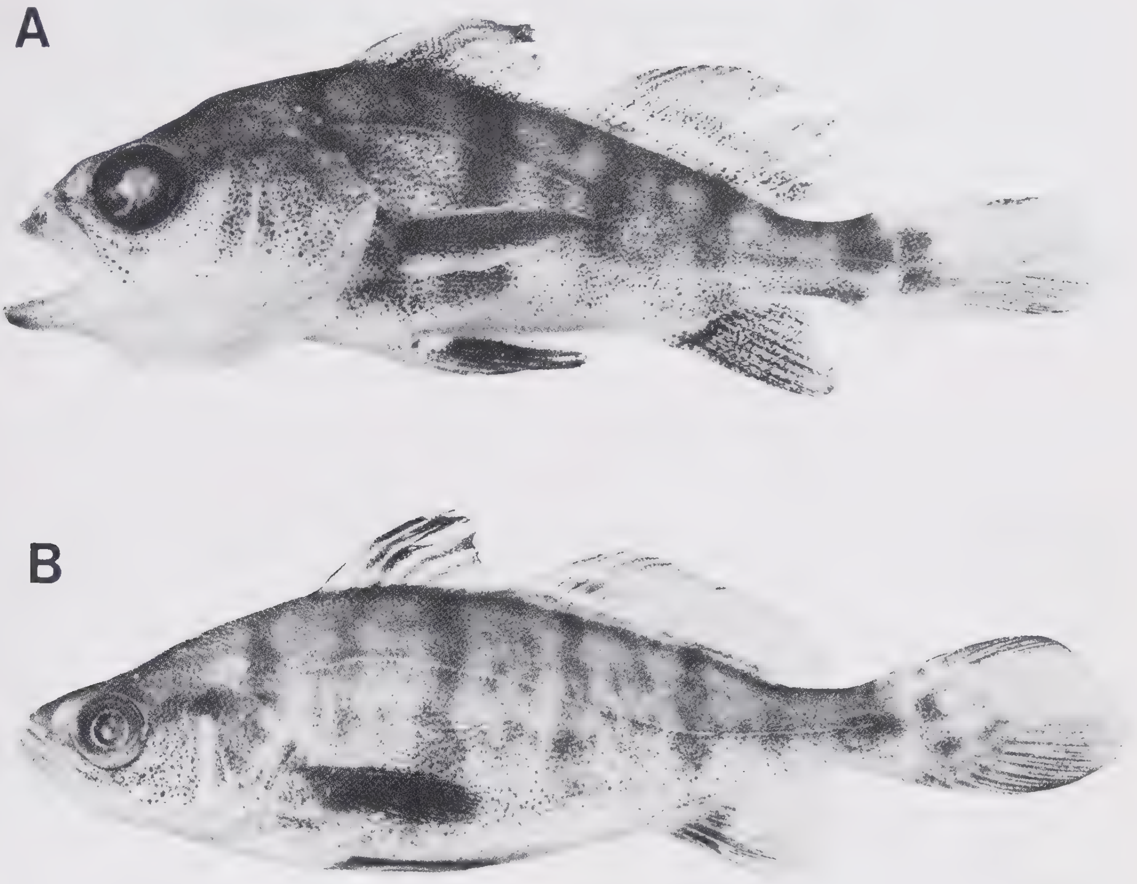

Figure 4. Juveniles of *Atractoscion nobilis*. *A*. 33.5 mm SL, day 72, from April 12, 1982, spawning. *B*. 64.5 mm SL, day 103, from January 26, 1983, spawning.

During the remainder of the preflexion period the body sheath extends posteriad to almost midway on the tail, and pigment increases on the pectoral fin. During notochord flexion the body sheath progresses posteriad; pigment increases on the pectorals; and pigment begins to appear on the developing anterior dorsal fin and the pelvic fin.

In postflexion larvae the body sheath continues to expand posteriad, and the rapidly enlarging paired fins become heavily pigmented, as does the spinous dorsal fin. At about 10.0 mm SL, only the caudal peduncle and the caudal, soft dorsal, and anal fins remain unpigmented. A pigment patch appears at the base of the caudal fin (at ca. 10 mm), over the hypurals, and expands to meet the body sheath; thus the body is completely covered by ca. 15 mm. Pigment extends onto the bases of the soft dorsal and anal fins, but the caudal fin remains unpigmented until after the larval period.

Vertical pigment bands are usually present in *A. nobilis* as small as 10.5 mm SL (Figure 3B). The nape band and a band under the middle of the first dorsal fin (spines 5-9) are the first to appear. These are soon followed by a band under the middle of the second dorsal fin (rays 13-16), and at this stage the heavily pigmented caudal fin base also has the appearance of a band (Figure 3C). Some late-flexion larvae have a band under the anterior portion of the second dorsal fin (rays 3-7). Four intermediate bands or saddles develop between these 5 primary bands in juveniles, but these are fainter and narrower than the primary bands (Figure 4).

TABLE 6

Development of Head Spines (Left Side) in Postflexion Larvae of *Cynoscion acoupa maracaiboensis*

Bone	Location	Number of spines Body length (mm) 6.9	7.5	8.3	8.4	9.8	10.3	10.7	13.5	14.2
Preopercle	Anterior series	3	4	4	6	4	5	4	7	8
	Posterior series	3	4	4	5	4	4	4	4	5
Opercle		—	—	—	1	2	2	2	2	2
Subopercle		1	1	2	1	1	2	1	1	3
Interopercle		1	1	1	1	1	1	1	1	2
Posttemporal		1	1	2	1	3	5	2	6	8
Frontal	Supraocular	2	3	3	4	6	6	6	10	11
Pterotic		—	—	—	—	—	1	—	2	3
Scale Bone	Dorsal epiotic region	—	—	—	—	—	—	1	2	2
Scale Bone	Ventral epiotic region	—	—	—	—	—	—	—	3	3
Lacrymal		—	—	1	—	1	1	1	1	—
Dermospherotic		—	—	—	—	1	1	—	1	1
Circumorbitals		—	—	—	—	—	—	—	—	+

Comparison with Related Genera

Early life stages of *A. nobilis* differ markedly from those of 5 species of *Cynoscion* described in the literature: *C. acoupa maracaiboensis*[2]; *C. leiarchus* (Sinque 1980); *C. nebulosus* (Hildebrand and Cable 1934; Fable et al. 1978; Powles and Stender 1978); *C. nothus* (Hildebrand and Cable 1934; Powles and Stender 1978); *C. regalis* (Welsh and Breder 1923; Pearson 1941; Powles and Stender 1978); *C. striatus* (Weiss 1981). Egg diameters—known for *C. acoupa* (0.79-0.89 mm), *C. nebulosus* (0.70-0.85 mm), and *C. regalis* (0.80-1.05 mm)—are smaller than in *A. nobilis*. *Cynoscion* species, with the exception of *C. nebulosus*, are lightly pigmented at hatching, and first-feeding larvae have melanophores along the dorsal and ventral midlines, over the dorsal surface of the gut, and on the head, usually at the opercular region. With the exception of *C. nebulosus*, dorsal midline pigment is soon lost, and pigment is added to the head and over the body in patches that form vague bars in postflexion larvae. In *C. nebulosus* the dorsal and ventral midline pigment intensifies with development, as does a prominent lateral pigment line that extends along most of the body and forward as internal head pigment. This becomes a prominent irregular stripe in postflexion larvae and in juveniles.

As in *Atractoscion*, *Cynoscion* larvae develop a large bulbous head with large jaws; however, the snout and gut are shorter in *Cynoscion*. The body is rounded in cross section and tapers gradually posteriad from the head, contrasting with the deep, robust body form of *A. nobilis*. Larvae of *C. nebulosus* differ from other *Cynoscion* in having a more slender profile.

Series of postflexion larvae of *C. acoupa maracaiboensis* were measured and cleared and stained to compare morphometrics, head-spine development, and meristics with *A. nobilis* (Tables 5-7). Relative snout length, eye diameter, pectoral and pelvic fin length are markedly smaller in *C. acoupa*. Spines de-

TABLE 7

Meristics of Postflexion Larvae of *Cynoscion acoupa maracaiboensis*

Body length (mm)	Dorsal fin rays	Anal fin rays	Pectoral fin rays	Principal caudal fin rays	Procurrent caudal fin rays	Vertebrae	Branchiostegal rays	Pelvic rays
6.9	XIII + I,18	I,8	—	9 + 8	—	25	7	I,4
7.5	X + I,19	II,8	15	9 + 8	3 + 3	25	7	I,5
8.3	IX + I,21	II,8	12	9 + 8	3 + 3	25	7	I,5
8.4	X + I,22	II,8	17	9 + 7	6 + 5	25	7	I,5
9.8	X + I,19	II,8	16	9 + 8	6 + 5	25	7	I,5
10.3	X + I,19	II,8	17	9 + 8	6 + 5	25	7	I,5
10.7	X + I,20	II,8	16	9 + 8	7 + 6	25	7	I,5
13.5	X + I,20	II,8	17	9 + 8	9 + 8	25	7	I,5
14.2	X + I,19	II,8	18	9 + 8	10 + 9	25	7	I,5

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[2] Olivares, R. MS Observaciones preliminares sobre el desarollo de huevos y larvas vitelinas de la Curvina de Lago. *Cynoscion acoupa maracaiboensis* (Pisces Sciaenidae)

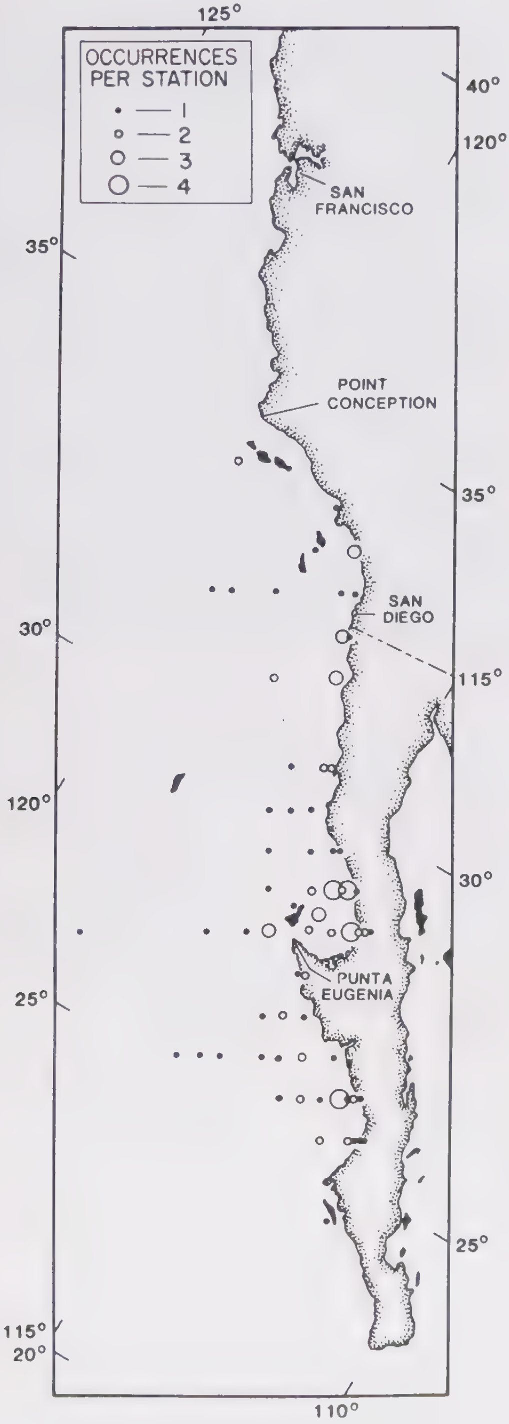

Figure 5. Occurrences of *Atractoscion nobilis* larvae in all CalCOFI samples taken from 1950 to 1978

velop on the same bones, but there are fewer spines on the preopercle and lacrymal compared with *A. nobilis*.

To our knowledge the only species of sciaenid with early stages similar to *A. nobilis* is *Sciaena umbra* from the eastern Atlantic, Mediterranean, and Black Sea (Montalenti 1937; Dekhnik 1973). Egg diameter is 1.15-1.30 mm, with an oil globule diameter of 0.23-0.30 mm (Dekhnik 1973). Larvae are 2.5-2.6 mm at hatching and develop a body form and pigment pattern very similar to that of *A. nobilis*. Late-stage larvae of the western Atlantic species, *Larimus fasciatus*, have large, heavily pigmented paired fins, but the body pigment is not a solid cloak as in *A. nobilis* (Hildebrand and Cable 1934).

DISTRIBUTION

Atractoscion nobilis larvae occurred in only 104 of all CalCOFI tows made during 1950-78. Of these, 98 occurrences were recorded in tows made in April-August in a coastal zone with a seaward limit to station 60. Only 2 occurrences were on stations seaward of station 60—station 120.90 on cruise 5106 and station 130.65 on cruise 5906. Latitudinal limits were from CalCOFI station 83.55 near the northern Channel Islands to station 143.26 near Santa Margarita Island and Magdalena Bay, Baja California (Figure 5). Fifteen percent of the white seabass occurrences were in southern California waters, and the remaining 85% were along Baja California, with 50% north and 35% south of Punta Eugenia. The highest concentrations of larvae were found in the inshore regions of Sebastian Viscaino Bay and San Juanico Bay, Baja California. *A. nobilis* larvae were collected from January-October, but 92% of the occurrences and 95% of the individuals were taken from May-August. The peak month was July, with 55% of the occurrences and 60% of the individuals.

The size-frequency distribution of the white seabass larvae collected during the CalCOFI sampling program was narrow, with a mean length of 3.4 mm ± 1.10 SD and a range of 1.6-7.2 mm in the 122 larvae measured. Latitudinal trends in spawning season could not be determined with this limited length-frequency data.

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Protandrous Hermaphroditism in Striped Bass from Coos Bay, Oregon

MIKE MOSER
Center for Coastal Marine Studies

JEANNETTE WHIPPLE
National Marine Fisheries Service
Southwest Fisheries Center
Tiburon, California 94920

JUDY SAKANARI AND CAROL REILLY
Center for Coastal Marine Studies
University of California
Santa Cruz, California 95064

Abstract

Eleven of 42 adult striped bass collected from Coos Bay, Oregon, were possibly protandrous. The older hermaphrodites, ages 7 to 10 years, showed increasing signs of pathology associated with egg retention.

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In the early 1880s, 500 striped bass *Morone saxatilis* were introduced from Navesink River, New Jersey, into San Francisco Bay, California. By the end of the nineteenth century, the species supported a thriving fishery in California. In 1914, striped bass were reported for the first time off the Oregon coast (Morgan and Gerlach 1950), presumably having migrated from San Francisco Bay. The Oregon population had grown to 15,000–20,000 fish by 1980 (R. Bender, Oregon Department of Fish and Wildlife, unpublished).

During a survey of parasite and pollutant burdens of striped bass in Coos Bay, Oregon, we had occasion to observe several cases of hermaphroditism, on which we report here. This phenomenon has been noted previously for the species. Morgan and Gerlach (1950) found that 3% of 124 striped bass from Coos Bay were hermaphrodites with functional testes and ovaries, the ovary being larger in some cases and the testis in others; the fish were not aged. Schultz (1931) also described an Oregon striped bass that could have spawned both sperm and eggs. Two cases of hermaphroditism were reported for the congeneric white perch *Morone americana* (Bishop 1920; Dorfman 1976). Dorfman found that a specimen from New Jersey had normal spermatozoa but immature ovaries. None of these authors reported any signs of pathology related to the hermaphroditism. Here, we report both age distributions and pathologies of hermaphroditic striped bass.

Methods

We worked with 42 prespawning striped bass gillnetted from Coos Bay 21–28 May 1980. In connection with our examinations for parasites and pollutants, we examined the gonads of fresh fish. Oviducts were probed for possible occlusions. Sperm were examined microscopically and released into fresh water to determine motility. Egg characters evaluated included diameter, color, development, and amounts of yolk, oil, and perivitelline space. Scales were used to age the fish.

Results and Discussion

Eleven of the 42 adult striped bass were hermaphrodites. Protandry is suggested because young hermaphrodites had ripe, motile sperm and immature eggs whereas older hermaphrodites had normal-appearing eggs and only small patches of testes (Table 1). The sex-ratio shift toward females as the fish aged may be an artifact of field collections because size and sex ratio may depend on sampling location and season (Setzler et al. 1980; Kohlenstein 1981) and because females usually live longer than males (Setzler et al. 1980). The hermaphrodites with small testes and large ovaries, ages 7 to 10 years, showed increased pathology associated with egg retention as annual egg masses were added and the abdominal organs became increasingly more encased in visceral adhesions (Fig. 1). The hermaphrodites had one or more ovarian ducts blocked by adhesions. This blockage, or hormones produced by the testes, may account for the retention of egg masses in the ovaries. In these hermaphrodites, ripe eggs were found in the outermost ovarian sacs. Each egg mass, representing previous spawning seasons, became progressively more degenerated towards the interior of the gonad (Fig. 1). Numerous small, hard, degenerated eggs were embedded in the visceral organs and peritoneum. The oldest hermaphrodites had more constricted stomachs and intestines (Fig. 1) and more swollen abdomens than normal prespawning females. The

TABLE 1.—*Distribution of 42 striped bass from Coos Bay, Oregon, among gender conditions, by age.*

		Hermaphrodites		
Age, years	Males	Large testes, small ovaries	Small testes, large ovaries	Females
4	9	0	0	0
5	0	1	0	0
6	0	0	0	2
7	0	1	1	0
8	3	0	4	5
9	0	0	0	1
10	1	0	4	2
13	1	0	0	2
14–19	0	0	0	5

four oldest hermaphrodites, 10 years old, had retained their eggs for up to 5 years. Female striped bass normally mature at age 4 or 5. The absence of hermaphrodites older than 10 years suggest that continual reabsorption of egg masses may prove fatal. Alternatively, if the Coos Bay fish are protandrous, the hermaphrodites may resorb their degenerative egg masses and become normal females. This distinction cannot be made without further field collections. If the hermaphrodites, whether protandrous or simultaneous, die as a result of the pathology associated with egg retention, this type of hermaphroditism may, in time, be selected against. However, in this relatively small, isolated, and recently established population, if a functional male hermaphrodite fertilizes normal females, or if a hermaphroditic female releases some eggs, this trait can be transmitted. In comparison, only two hermaphrodites were identified from more than 500 adult striped bass collected from the larger population in San Francisco Bay, which may reflect the larger gene pool or different environmental conditions in California.

In the past, the genus *Morone* periodically has been placed in the family Serranidae (Miller and Lea 1972), which contains species that undergo protogynous sex reversal. If striped bass are protandrous, this may be additional justification for the removal of this species from that family.

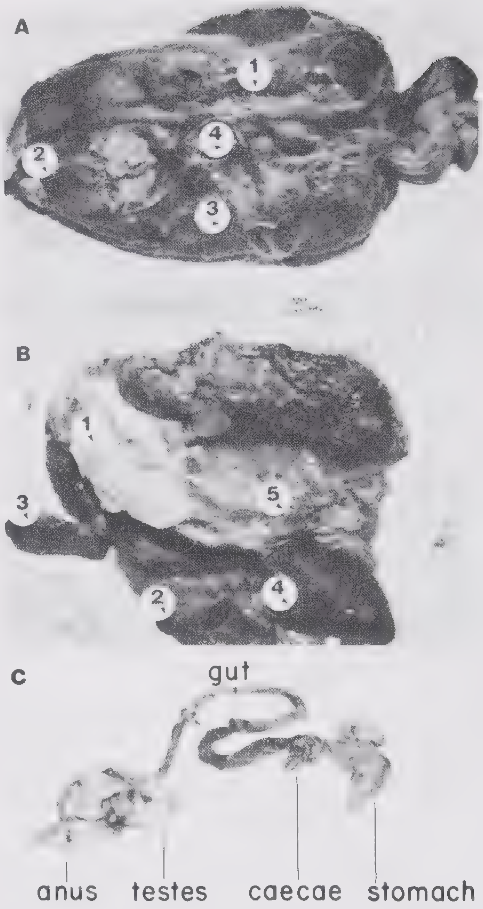

FIGURE 1.—*Gonads of a typical 10-year-old hermaphroditic striped bass.* **A.** *Digestive and reproductive tracts encased in visceral adhesion: (1) intestine; (2) ripe ovarian sac; (3–4) degenerated egg masses.* **B.** *Egg masses retained from previous spawns: (1) testes; (2) ripe eggs; (3–5) successive degenerated egg mass.* **C.** *Digestive and reproductive systems.*

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OCEAN SCALE AND REGIONAL COMPARISON - ESTUDIOS OCEANICOS Y COMPARACION REGIONAL

COMPARATIVE CLIMATOLOGY OF SELECTED ENVIRONMENTAL PROCESSES IN RELATION TO EASTERN BOUNDARY CURRENT PELAGIC FISH REPRODUCTION

by

Richard H. Parrish, Andrew Bakun, David M. Husby and Craig S. Nelson

Pacific Environmental Group
Southwest Fisheries Center
National Marine Fisheries Service, NOAA
P.O. Box 831
Monterey, California 93942
USA

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Resumen

Las principales regiones oceánicas del mundo con corrientes marinas en sus confines orientales (i.e., Sistemas de California, Perú, Canarias y Benguela) parecen comportar dinámicas ambientales similares y contienen congregaciones similares de especies de peces pelágicos. En la medida en que especies correspondientes a diferentes sistemas funcionen como análogos, los estudios comparativos interregionales pueden producir información relativa a los efectos del ambiente en el éxito de la reproducción. Lo que de otra forma sería difícil de obtener de un sólo sistema regional.

Los archivos históricos con informes del clima marino proporcionan una fuente de datos en formatos similares sobre la climatología de procesos oceánicos en varias regiones. Estos forman la base para reconocer las diferencias y semejanzas en las diversas áreas de desove de especies correspondientes. La selección natural implica que los hábitos reproductivos en cada caso representan la adaptación a los factores ambientales más cruciales. Por lo tanto los patrones de las relaciones de la reproducción y el ambiente sugieren la existencia de enlances de causalidad importantes.

Esta forma de deducir los factores ambientales que son cruciales puede dar una base racional para limitar las alternativas en cuanto a las variables que pueden explicar estos procesos. Permitiéndo de esta forma el uso más efectivo de las series de datos en la formulación de modelos donde el reclutamiento es dependiente de las condiciones ambientales. Además, el concentrarse en los principales interacciones stock - ambiente puede proveer las bases para utilizar la experiencia que se gana en un sistema para predecir el resultado de acciones en otro sistema.

Normalmente los datos sobre las variables causales primarias (alimento, predación, mortalidad dependiente de la densidad, etc) no están disponibles. Por lo tanto nos concentramos en varios procesos que pueden ser abordados usando datos del mar. Se piensa que estos procesos pueden tener un impacto en los estadios tempranos de la vida de los peces al alterar las variables causales primarias, particularmente el alimento. Estos incluyen: (1) mezcla por turbulencia generada por el viento, que puede dispersar las concentraciones de pequeña escala de las partículas de alimento necesarios para que las larvas se alimenten por primera vez en forma éxitosa; (2) transporte mar afuera, que puede arrastrar los huevos y larvas planctónicos fuera de las áreas costeras que le son favorables; (3) afloramientos costeros, que pueden ser favorables si se presentan con un retraso apropiado pero son perjudiciales si coinciden en espacio y tiempo con el desove. La temperatura es una variable causativa primaria por sus efectos directos sobre procesos fisiológicos.

Los cuatro principales sistemas de corrientes de los confines orientales del mar tienen mucho en común. La ubicación y estacionalidad del máximo transporte Ekman mar afuera parece estar estrechamente relacionado con el desplazamiento latitudinal y estacional de los sistemas de presión atmósferica y con las relaciones entre estos sistemas y la topografía de los continentes. Sin embargo, como se puede ver de las características ambientales que se presentan, hay también grandes diferencias entre ellas. Por ejemplo, los cuatro sistemas tienen anomalías máximas de bajas temperaturas mar afuera mar adento, asociadas con el máximo transporte mar afuera de Ekman de varano. En estas regiones de máximos afloramientos de verano se encuentran stocks de anchoveta y/o sardina con áreas de desove desplazadas hacia el polo y hacia el ecuador. Los sistemas de California y de Benguela tienen, ambos, una sóla área con anomalías superficiales de baja temperatura. En el sistema de California esta área está ubicada en el área de máximo afloramiento de verano, mientras que el sistema de Benguela tiene un área de afloramiento máxima de verano en Luderitz y un área de afloramiento máximo de invierno en Cabo Frío. Los sistemas de Perú y las Canarias tienen cada uno dos áreas separadas de anomalías superficiales de baja temperatura. El sistema peruano tiene un área localizada en el área de máximo afloramiento de invierno (San Juan o Chimbote) y una segunda área en la zona de afloramiento frente a la parte central de Chile, que tiene un máximo de verano en Talcahuano. El sistema de Canarias tiene un afloramiento máximo de verano frente a Lisboa y un segundo afloramiento máximo de verano entre Cabo Sim y Cabo Blanc. Durante el invierno la anomalía de aguas frias frente al noroeste de Africa se desplaza al sur y el máximo del afloramiento se extiende de Cabo Blanc a Cabo Vert.

Los centros de afloramiento (caracterizados por un fuerte transporte mar afuera, intensa mezcla por turbulencia generada por el viento, y reducida estabilidad de la columna de agua) parecen ser evitados como parte de los hábitos de desove. Las áreas de desove de anchovetas y sardinas tienden a estar en las áreas costeras donde el transporte y turbulencia inducidos por el viento son reducidos y la plataforma continental tiende a ser más amplia. Las áreas de desove de las poblaciones más grandes tienden a estar corriente abajo (hacia el ecuador) con respecto a los centros de afloramiento. La población de anchoveta (que ha sido el más grande de todos los stocks actuales de sistemas de corrientes de los confines orientales del mar) desova en un área de fuerte afloramiento. Nuestra hipótesis es que en este caso el ambiente costero particularmente amplio, y la dependencia de la profundidad de la capa de Ekman de la latitud y la estratificación puede servir para reducir el efecto perjudicial del transporte superficial mar afuera de Ekman.

Los patrones para evitar la mezcla por turbulencia y el transporte mar afuera en los hábitos reproductivos sugieren que estos procesos han ejercido un importante control sobre el éxito de la reproducción. Aparentemente estas variables merecen ser consideradas al modelar las variaciones del reclutamiento. En regiones donde las temperaturas características se encuentran dentro de límites fisiológicos, la temperatura no parece ser un factor dominante al determinar el ambiente para el desove.

La capa mínima de oxígeno frente al Perú es muy superficial en comparación con otras regiones. Se sugiere que esto puede conducir a menor competencia entre los stocks de peces pelágicos y los mesopelágicos.

INTRODUCTION

In this work we have developed climatological fields of oceanographic and meterological data for the four "classical" eastern boundary current systems (Wooster and Reid, 1963). We attempt, through pattern recognition, to define similarities and differences in the characteristic environmental conditions in the spawning grounds of the recognized stocks of pilchard (Sardina and Sardinops) and anchovy (Engraulis) in these systems. Our approach is similar to Reid's (1967) analysis of the oceanic environs of the genus Engraulis. He included the entire life cycle and described the range of surface temperature and salinity in which Engraulis occurs. We have limited our comparisons to the environments in which the early life history stages occur (i.e., the spawning grounds) and have expanded the list of environmental variables.

A major motivation for international cooperation in fisheries research is the assumption that research methods and/or results derived from studying one population can be transferred to another. For example, the recently proposed "International Recruitment Experiment" (IREX)[2] is based on the hypothesis that the biological responses to environmental conditions are similar for separate stocks of closely related species. The IREX proposal identifies six variables which are thought to account for most of the biological variability observed in exploited fishes. These variables are temperature, turbulence, transport, food, predation, and population density. Population variations of stocks within a species group, or even in an individual stock, could be caused by any, or all, of the six variables. The hypothesis does not imply that different stocks of a given species group have the same environmental variable as their limiting factor. Rather it implies that the stocks have a similiar functional relationship to that environmental variable.

In this work we are addressing a narrow subset within the IREX construct. The species groups considered are anchovies and pilchards, and we are limiting the analyses to comparisons of the environments of their spawning grounds in the four major eastern boundary currents. The regions of interest consist of the California Current off western North America, the Peru Current off western South America, the Canary Current off the Iberian Peninsula and northwestern Africa, and the Benguela Current off southwestern Africa (Fig. 1). Data which could be used to compare the predation, food, and density variables are not available for the spawning grounds of most of the stocks in the California, Peru, Canary, and Benguela Currents. We are therefore basing our comparisons upon several processes which can be indicated by available maritime data. These processes are thought to have important impacts on the early life history of the two species groups by altering the primary causative variables, particularly food. From the point of view of the utility of the study, results based on routinely available data offer the possibility of being followed in real time for management purposes.

Eastern boundary currents are characterized by equatorward surface flow and coastal upwelling. One result of these factors is that the eastern sides of the oceans have a very extensive temperate zone. For example, the 20° and 10°C isotherms at 10 meters occur at lat. 27°N and 60°N in the eastern North Pacific, and in comparison they occur at lat. 40°N and 45°N in the western North Pacific (Barkley, 1968). Another feature of eastern boundary current regions is the tendency for narrow continental shelves. Consequently the fisheries of eastern boundary currents are dominated by a small number of temperate pelagic fishes which can achieve very large populations. The physical environments of the four major eastern boundary currents are quite similar and therefore it is not surprising that their fisheries are dominated by very closely related, geographically isolated stocks or species (Table 1). Pilchards, anchovies, jack mackerel (Trachurus), and hake (Merluccius) achieve the largest populations; mackerel (Scomber japonicus) and bonito (Sarda) also are important in the fisheries of the eastern boundary currents, although they don't attain the population size of the other four species groups.

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[2] Report of Scientific Committee on Ocean Research (SCOR) and Advisory Committee of Experts on Marine Resources Research (ACMRR), Working Group 67 (Oceanography, Marine Ecology and Living Resources) developed in response to the Ocean Sciences in Relation to Living Resources (OSLR) resolution of the Intergovernmental Oceanographic Commission (IOC), 1 July 1982.

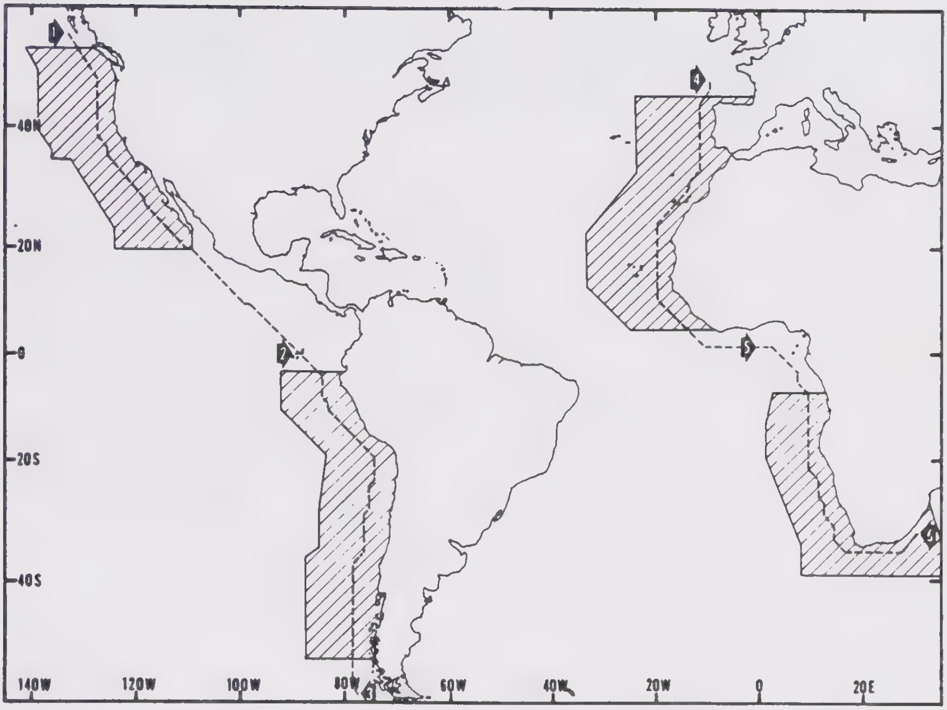

Figure 1. Geographical orientation of various summaries presented in this paper. Appendix maps are assembled from summaries within 1-degree areal segments of the four eastern boundary current regions indicated by diagonal hatching. Alongshore vertical sections (Figs. 3-6) are arranged along the dashed lines near the eastern ocean boundaries.

TABLE 1. Dominant anchovy, pilchard, horse mackerel, hake, mackerel, and bonito in the four major eastern boundary currents (after Bakun and Parrish, 1980).

CALIFORNIA CURRENT	PERU CURRENT	CANARY CURRENT	BENGUELA CURRENT
Engraulis mordax	*Engraulis ringens*	*Engraulis encrasicholus*	*Engraulis capensis*
Sardinops sagax	*Sardinops sagax*	*Sardina pilchardus*	*Sardinops ocellatus*
Trachurus symmetricus	*Trachurus symmetricus*	*Trachurus trachurus*	*Trachurus trachurus*
Merluccius productus	*Merluccius gayi*	*Merluccius merluccius*	*Merluccius capensis*
Scomber japonicus	*Scomber japonicus*	*Scomber japonicus*	*Scomber japonicus*
Sarda chiliensis	*Sarda chiliensis*	*Sarda sarda*	*Sarda sarda*

Fisheries for pilchards and anchovies are notorious for their extreme variability. All four current systems at one time or another have had fisheries dominated by pilchards (Fig. 2). The northern stock in the California Current system (Radovich, 1981) and the Namibian (Troadec, Clark, and Gulland, 1980) and South African (Cram, 1981) stocks in the Benguela Current system have collapsed under heavy exploitation. The Peru Current system (Serra et al., 1979) and the Canary Current system (FAO, 1978) have had recent increases in the size of pilchard stocks, and landings in these regions are presently dominated by pilchards. Conversely, anchovies presently dominate the landings in the Benguela and California Current systems and appear to be abundant, although lightly exploited in the Canary Current system. The collapse of the Peru anchoveta stock under heavy exploitation is well known (Tomczak, 1981).

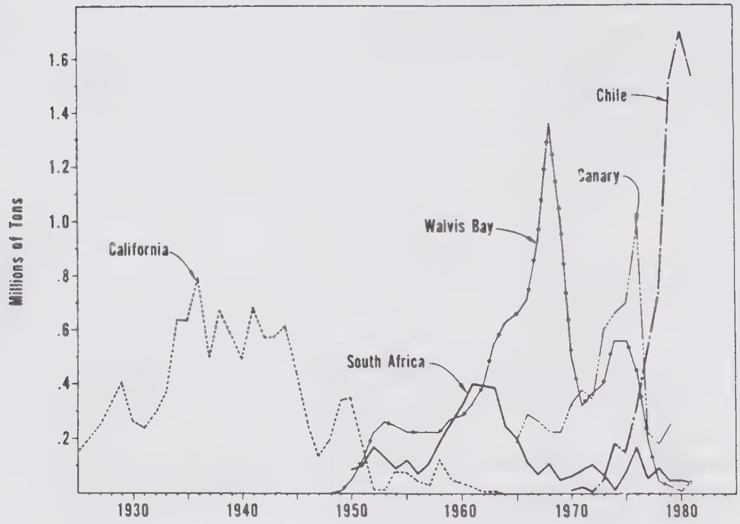

Figure 2. Yearly pilchard (sardine) landings from several eastern boundary current stocks.

The basis for our comparison is, like the IREX proposal, dependent upon the hypothesis that closely related stocks or species have similar early life history requirements. This would suggest that the environments of the various spawning grounds are similar. That is, in the mean they should fall within the tolerance range of the species group. This does not imply that environmental conditions in the spawning grounds are optimal, only that stocks have recently maintained populations by spawning there.

How unrelated may the stocks be before this hypothesis becomes ridiculous? Most fisheries biologists would probably agree[3/] that the present California stock of pilchard (sardine) has the same physiological requirements as the stock had in the 1930's before it collapsed. However, the present remnant of the stock may have a different gene pool than the original. Most fisheries biologists would probably agree[3/] that, within a given species, physiology is nearly identical. Taxonomic distinctions at the species-generic level are quite plastic. The mackerel stocks of the eastern boundary currents are now considered to belong to the same species, Scomber japonicus. Just a few years ago they were considered to be different species and the genus was not Scomber but Pneumatophorus. Each eastern boundary current presently has a different species of Engraulis. These "species" are very similar and it takes considerable expertise to tell them apart. To quote McDowell (1962), "There are grounds for suspicion that this expertise is not possessed by the fish themselves...." We are assuming that in the case of geographically separated stocks of closely related species the differences in the physiological requirements of the early life history stages are negligible.

To provide a basis for our comparisons, historical subsurface oceanographic data and surface marine weather observations are used to examine the large-scale spatial and seasonal patterns of several environmental parameters which appear to have had important effects on the spawning habits of pelagic fishes in eastern boundary current systems. Our comparative studies are primarily focused on the atmosphere-ocean processes related to horizontal and vertical advection, vertical stability, and temperature. Bakun and Parrish (1980) discussed the rationale for selecting the particular suite of oceanic and atmospheric properties described in this study.

Characteristic annual mean distributions of oceanographic data and summer and winter climatologies based on surface marine weather observations are presented in the Appendix as charts of surface geostrophic flow, sea surface temperature and coastal temperature anomaly, surface wind-driven transport, an index of wind-generated turbulent mixing, and total cloud amount. The methods used to compile the climatological data are summarized in the Appendix. The format of placing the charts in an appendix, rather than in the text, was selected to facilitate simultaneous intra- and interregional geographic and seasonal comparisons of the large-scale oceanographic and atmospheric properties.

[3/] A hedge word is always necessary when discussing what fisheries biologists will agree upon.

REGIONAL ASPECTS

The surface flow field in eastern boundary current systems, at least on the time and space scales affecting reproductive success of fish stocks (Parrish, Nelson, and Bakun, 1981) can be considered to be a combination of the surface Ekman drift (i.e., the transport of surface waters under the direct action of the wind) and the underlying geostrophic flow field. Highly smoothed representations of the geostrophic flow patterns in the four regional systems (Appendix Chart 1) show major common features. Near the coast, large-scale flow is generally equatorward. At high latitudes the tendency is poleward. Within several hundred kilometers of the coast, a component of large-scale geostrophic flow toward the coast is a common feature. The far offshore regions are characterized by flow toward the coast in the higher-latitude west wind drifts, weak equatorward flow at mid-latitudes, and flow toward the ocean interiors in tropical regions.

Coastal temperature anomaly patterns (Appendix Charts 5 and 6) indicate a general tendency for cool coastal temperatures relative to those offshore. These patterns show local centers of intense cooling associated with coastal upwelling. There also are relatively warm areas within coastal indentations (responding to seasonal warming) and at the high latitude extremes of the regions (associated with warm advection in the poleward flows).

Surface Ekman transport (Appendix Charts 7 and 8) is generally offshore, but becomes onshore at higher latitudes during the winter seasons. Wooster and Reid (1963) have demonstrated that the major geographical and seasonal features of eastern boundary coastal cooling can be related to corresponding features in offshore Ekman transport. Major capes, marking substantial changes in large-scale coastline trend, tend to be regions of maximum offshore Ekman transport and of associated upwelling and coastal cooling.

GEOSTROPHIC CURRENT CHARACTERISTICS

The common large-scale features of the eastern boundary currents have been described by Wooster and Reid (1963). The surface flow in these large systems is predominantly in the sense of the prevailing winds, which is anticyclonic about the mid-ocean atmospheric high pressure cells. The weak (typically less than 50 cm sec^{-1}) equatorward geostrophic flow in eastern boundary currents is due to the baroclinicity of a relatively shallow layer, generally confined to the upper 500 m (Wooster and Reid, 1963).

Another common feature of eastern boundary currents is a poleward flowing undercurrent, which is a subsurface current usually centered at 200-300 m near the continental shelf edge. The waters transported poleward by the undercurrents appear to be enhanced by coastal upwelling and may contribute water to the upwelling centers (Smith, 1978). A poleward countercurrent may occur seasonally at the surface during the winter and during periods when the equatorward wind stress weakens.

Coastal countercurrents are often part of semi-permanent eddy circulations, for example, the Southern California Eddy (Sverdrup and Fleming, 1941). A permanent cyclonic circulation over the continental slope and shelf between Cape Frio and south of Lüderitz in southwest Africa has been postulated by Nelson and Hutchings (MS). In the Canary Current region a cyclonic circulation has been observed in the shallow Banc d'Arguin region south of Cap Blanc (Mittelstaedt, 1974) and may be seen in the schematic diagrams of Rebert (1978).

In addition to the narrow coastal currents and the poleward undercurrents, the large-scale surface circulation in eastern boundary current systems is complicated by the effects of bottom topography and coastline orientation. The advent of satellite infrared imagery of the sea surface and intensive hydrographic surveys in the upwelling regions have identified the existence of many eddy-like features or intense frontal zones associated with upwelling sites or downstream of capes and headlands (Bernstein, Breaker, and Whritner, 1977).

California Current System

The major features of the California Current system have been described by Reid, Roden, and Wyllie (1958), Pavlova (1966), and Hickey (1979). The cool, low salinity waters of the west wind drift diverge at about lat. 45°N, one branch flowing north to feed the Alaskan Current and the other branch flowing southeastward to become the California Current. The equatorward flow between lat. 45°N and 20° N and within about 500 km of the west coast encompasses the bulk of the California Current. Maximum equatorward flow occurs approximately 200-400 km from the coast and is strongest in the summer and early fall. A portion of the California Current turns into the coast at about lat. 30°N and is associated with negative wind stress curl in this region (Nelson, 1977). There is a relatively permanent northward flow near the coast between lat. 30°N and Point Conception (lat. 35°N) which forms the eastern portion of the Southern California Eddy in the Southern California Bight.

The California Undercurrent is a poleward flow of warm, relatively high salinity water at depths of approximately 250-300 m which lies close to the continental slope (Wooster and Jones, 1970). This current is present along the coast from southern Baja California to Vancouver Island (Reed and Halpern, 1976). The northward flow at the surface occuring during the fall and winter along the coast north of Point Conception is commonly called the Davidson Current.

Peru Current System

The north-northwestward flow north of lat. 40°S has been labelled the Peru or Humboldt Current. Gunther (1936) first recognized two branches of this current: a Peru Coastal Current and a Peru Oceanic Current. The northward flow generally splits into the Coastal and Oceanic Currents at about lat. 25°S (Wyrtki, 1965). The annual mean geostrophic flow (Appendix Chart 1) shows this bifurcation at lat. 25°S, long. 76°W and a component of the flow is directed onshore. Both the coastal and oceanic portions of the Peru Current originate in the sub-Antarctic region and transport cold, relatively low salinity water equatorward.

The Peru Countercurrent flows southward at about long. 80°W between the Peru Coastal Current and the Peru Oceanic Current. It is primarily a subsurface current with the strongest flow near 100 m.

The Peru Coastal Current coincides approximately with the upwelling region off Peru and Chile. Coastal bathymetry appears to have considerable influence on the current. Eddies are found wherever the coastal current is deflected strongly from the coast, especially near lat. 15°S (Cañon, 1978). The annual mean surface geostrophic flow is directed onshore north of lat. 15°S and flows strongly onshore in the coastal region between lat. 10°S and 12°S. Wooster and Sievers (1970) noted that the surface drift currents at the coast showed a minimum in equatorward flow between lat. 12°S and 14°S in all seasons, except summer.

During the austral winter the southeast trade winds reach maximum intensity. From April to September the Peru Current appears stronger than in other months and the countercurrent virtually disappears. At this time the two branches of the Peru Current coalesce and the contribution to the South Equatorial Current is the strongest.

The Peru-Chile Undercurrent is a narrow southward flowing countercurrent beneath the Peru Coastal Current. It is found offshore north of lat. 15°S, but south of lat. 15°S it follows close to the coast and can be identified as far as lat. 48°S (Silva and Neshyba, 1979). It is characterized by a low oxygen content.

Canary Current System

The large-scale geostrophic flow in the Canary Current region shows an equatorward component between about lat. 36°N and 20°N. The Canary Current leaves the coast in the vicinity of Cap Blanc (lat. 21°N), which is also the location of persistent upwelling. Cap Blanc is the site of a semi-permanent frontal zone between the North Atlantic Central Water advected southwest by the Canary Current and a low salinity South Atlantic Central Water mass which flows northward along the coast (Hughes and Barton, 1974).

During periods of weak northerly winds, which occur particularly in summer and autumn between lat. 10°N and 20°N, a coastal northwest-flowing countercurrent may be observed (Mittelstaedt, 1974). This coastal countercurrent gives rise to a cyclonic circulation over the shallow Banc d'Arguin south of Cap Blanc. The coastal countercurrent may be a response to the large discharge of fresh water during the summer from the Gambia and Senegal rivers.

Hughes and Barton (1974) found evidence of a northward flow at a depth of about 250 m extending from Cap Vert to Cabo Bojador. This poleward undercurrent was indicative of a narrow stream of cool, low salinity water flowing parallel to the continental shelf edge.

Benguela Current System

The major large-scale geostrophic currents off southwest Africa are the equatorward flow between lat. 35°S and about lat. 20°S, which is called the Benguela Current, and the primarily westward flowing Agulhas Current, which flows along the coast of south Africa to approximately long. 20°E where it is deflected to the south and east by the confluence with the west wind drift. A portion of the flow continues toward the northwest around Cape Agulhas and feeds a semi-permanent coastal jet between Cape Agulhas and Cape Columbine (Bang and Andrews, 1974). The principal features of the Benguela Current are described by Hart and Currie (1960).

The Benguela Current consists of the cool upwelled water found within 150 km of the west coast between lat. 15°S and 34°S (Shannon, 1970). In general, it flows northward, roughly following the isobaths between lat. 34°S and 23°S, while north of lat. 23°S it tends to veer away from the coast. Closer inshore a southward moving countercurrent has been occasionally recorded. Hart and Currie (1960) deduced the presence of a southward undercurrent on the continental slope off the Namibian coast from the downwarping of the mid-depth isopycnal surfaces as they approached the continental slope.

The existence of a relatively permanent cyclonic circulation over the continental slope and shelf regions between Cape Frio and a point just south of Lüderitz has been noted by Nelson and Hutchings (MS). The cyclonic circulation is comprised of the northwesterly jet-like flow southwest of Lüderitz where the flow of the Benguela Current accelerates towards the gap in the Walvis Ridge, and a southward return flow near the coast between Cape Frio and Lüderitz. The southward flow near the coast below 30 m has been reported by many investigators. Surface dynamic topography patterns from a series of monthly hydrographic cruises in this area in 1959-61 showed many instances of cyclonic gyres in the region between lat. 25°S and 20°S and southward geostrophic flow north of Lüderitz during spring and summer (Stander, 1964).

DISSOLVED OXYGEN

Minimum oxygen layers are associated with eastern boundary currents. These minimum layers are shallowest and most pronounced in the lower latitudes and more extensive and pronounced in the Pacific than in the Atlantic (Figs. 3, 4). For large-scale comparison of dissolved oxygen and its relationship to the upper mixed layer we developed annual dissolved oxygen and density (sigma-t) sections from data summarized by 1-degree squares. The sections are situated several degrees offshore to allow continuous deep-water sections. This procedure introduces some bias in relation to smaller scale, nearshore features. For example, coastal upwelling or other circulation processes may result in intrusions of low oxygen water into shallower depths on the shelf, which are not indicated by our offshore sections. These intrusions are most likely to occur in the lower latitude areas which are closer to the low oxygen sources. Such intrusions have been reported in the Benguela (Stander and de Decker, 1969) and Peru Currents (Guillén, 1980).

In the California, Canary, and Benguela Currents the minimum oxygen level is altered significantly in the vicinity of the subtropical convergences. The low latitude boundaries of these regions are marked by sharp sigma-t gradients associated with the subtropical convergences (Figs. 5, 6). They occur at about lat. 3°S in the Peru Current, lat. 17°S in the Benguela Current, lat. 22°N in the Canary Current, and lat. 25°N in the California Current. The upwelling regions of the eastern boundary currents are also apparent in the density sections; there are few sigma-t surfaces intercepting the surface in the upwelling regions. Equatorward of the convergences there is a sharp dissolved oxygen gradient associated with the thermocline and low dissolved oxygen values occur very near the surface. In the Canary and Benguela systems the minimum oxygen layers deepen and disappear in the vicinity of the subtropical convergences (i.e., at about lat. 20°N and 20°S). In the California Current system the minimum oxygen layer deepens significantly near the subtropical convergence; however, an extensive minimum oxygen layer extends throughout the entire system. Throughout the California Current system low oxygen levels (i.e., less than 2 mL L^{-1}) occur at about 300 m and the oxygen minimum layer occurs at 700-900 m.

The Peru Current is significantly different from the other three currents with respect to dissolved oxygen. The subtropical convergence occurs much closer to the equator and the low oxygen layer expands and shoals in the vicinity of the convergence. The oxygen minimum is at about 300 m throughout the Peru Current system. Off Chimbote, very low dissolved oxygen levels occur just beneath the upper mixed layer. However, at Coquimbo oxygen concentrations of 2 mL L^{-1} occur at about 300 m; this is similar to the California Current situation.

Low oxygen concentration could affect reproduction of pelagic fishes through reduction of growth rates of either larvae or adults (Pauly, 1981). It could also increase mortality rates by concentrating the adults or larvae to narrow layers near the surface where they might be more susceptible to predation. However, the "worst" dissolved oxygen conditions occur in the spawning areas of the Peruvian stocks which, at least in the case of Engraulis, lie in the most productive region. The other areas most likely to be influenced by low oxygen concentrations are the spawning areas of the Namibian stocks near Palgrave Point in the Benguela Current, and the Chilean stock, which has spawning grounds near Arica. These two areas are the next most productive regions after Peru.

We see two possible explanations for the association of low oxygen concentration and high pelagic fish productivity. Low oxygen concentration is associated with high nutrient concentrations. Low oxygen concentrations near the thermocline might therefore be associated with high primary production; more primary production, hence more fishery production. The other explanation concerns competition. Extensive egg and larval surveys have been made off Peru and California. Ahlstrom (1965) showed that mesopelagic fishes and hake accounted for about 22 percent and 17 percent, respectively, of the total larvae taken off California during the 1955-58 surveys. Both mesopelagic fishes and hake have their greatest abundance below the thermocline (Ahlstrom, 1959). Off Peru mesopelagic fishes and hake comprised only 4.1 and 0.37 percent of the larvae taken during 1966-68 (Santander and de Castillo, 1979). Anchovy larvae comprised 37 percent of the larvae in the California surveys and 92 percent in the Peruvian surveys. The very low oxygen levels just beneath the thermocline off Peru would be expected to severely limit the habitat space for hake and mesopelagic fishes. Habitat space for mesopelagic fishes in the California and Canary systems and most of the Benguela system is extensive and large stocks in these areas would be expected to be in competition with epipelagic fishes for food.

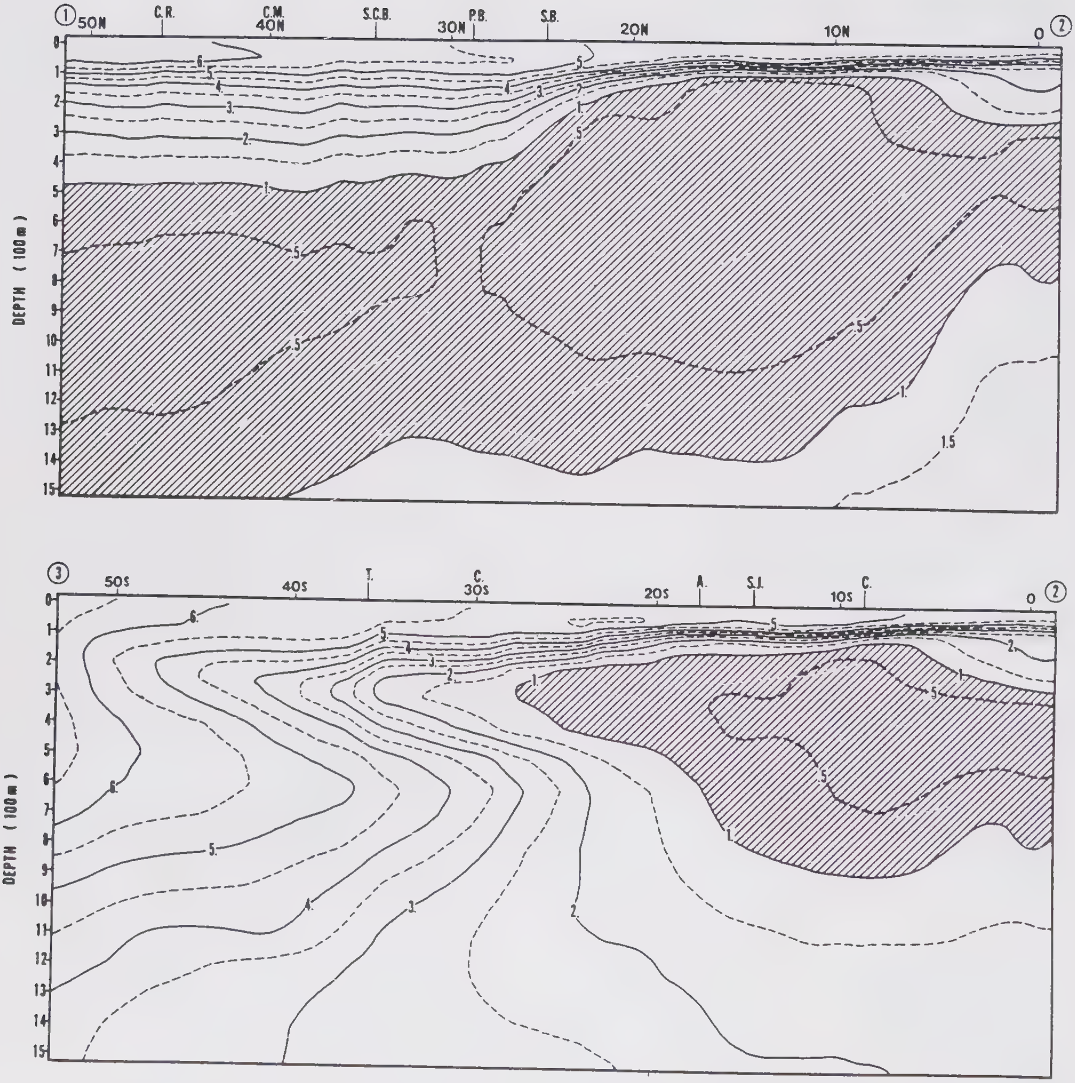

Figure 3. Dissolved oxygen (mL L^{-1}) vs. depth along the eastern boundary of the Pacific Ocean. The orientation of the section is shown in Figure 1. Initials at the top of the diagram indicate the latitudinal positions of locations discussed in detail in Section III of this paper.

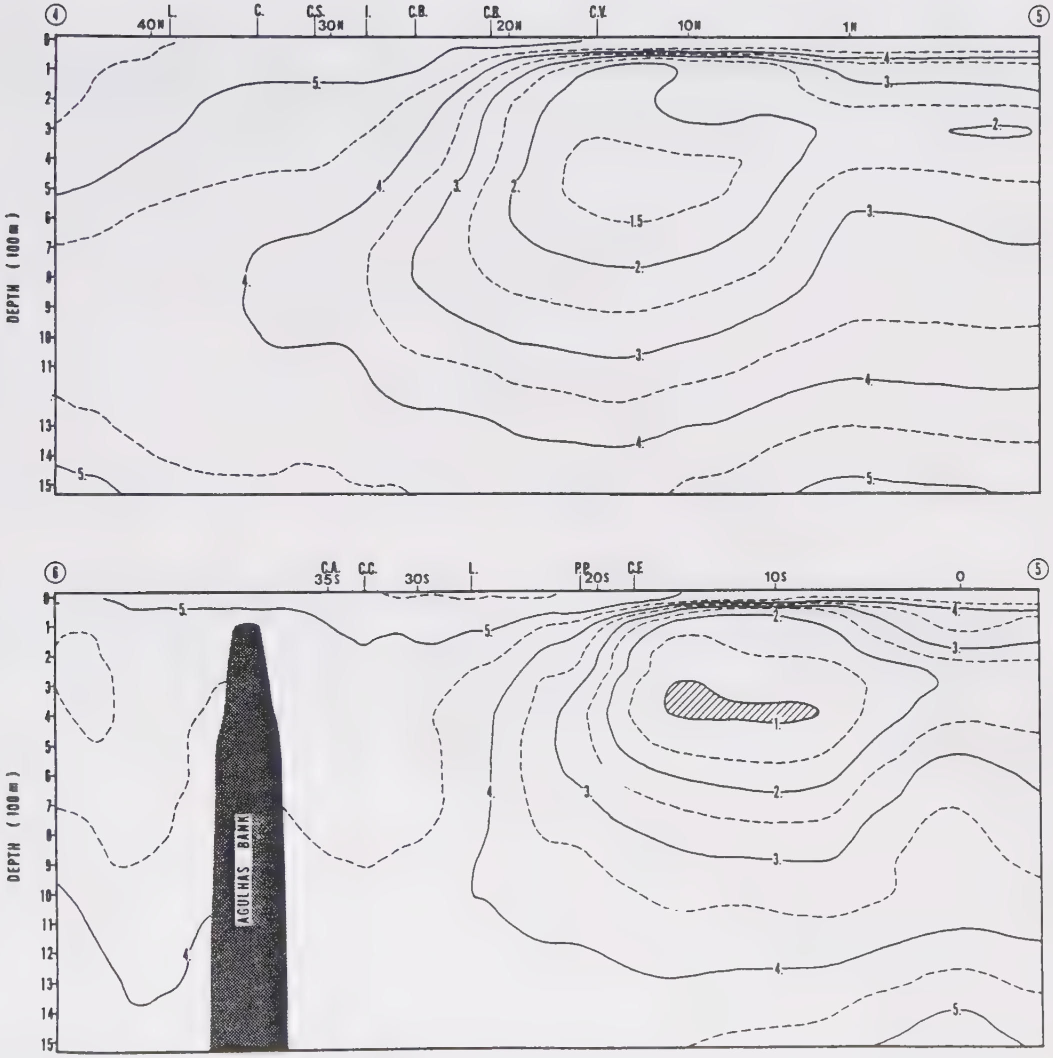

Figure 4. Dissolved oxygen (mL L^{-1}) vs. depth along the eastern boundary of the Atlantic Ocean. The orientation of the section is shown in Figure 1. Initials at the top of the diagram indicate the latitudinal positions of locations discussed in detail in Section III of this paper.

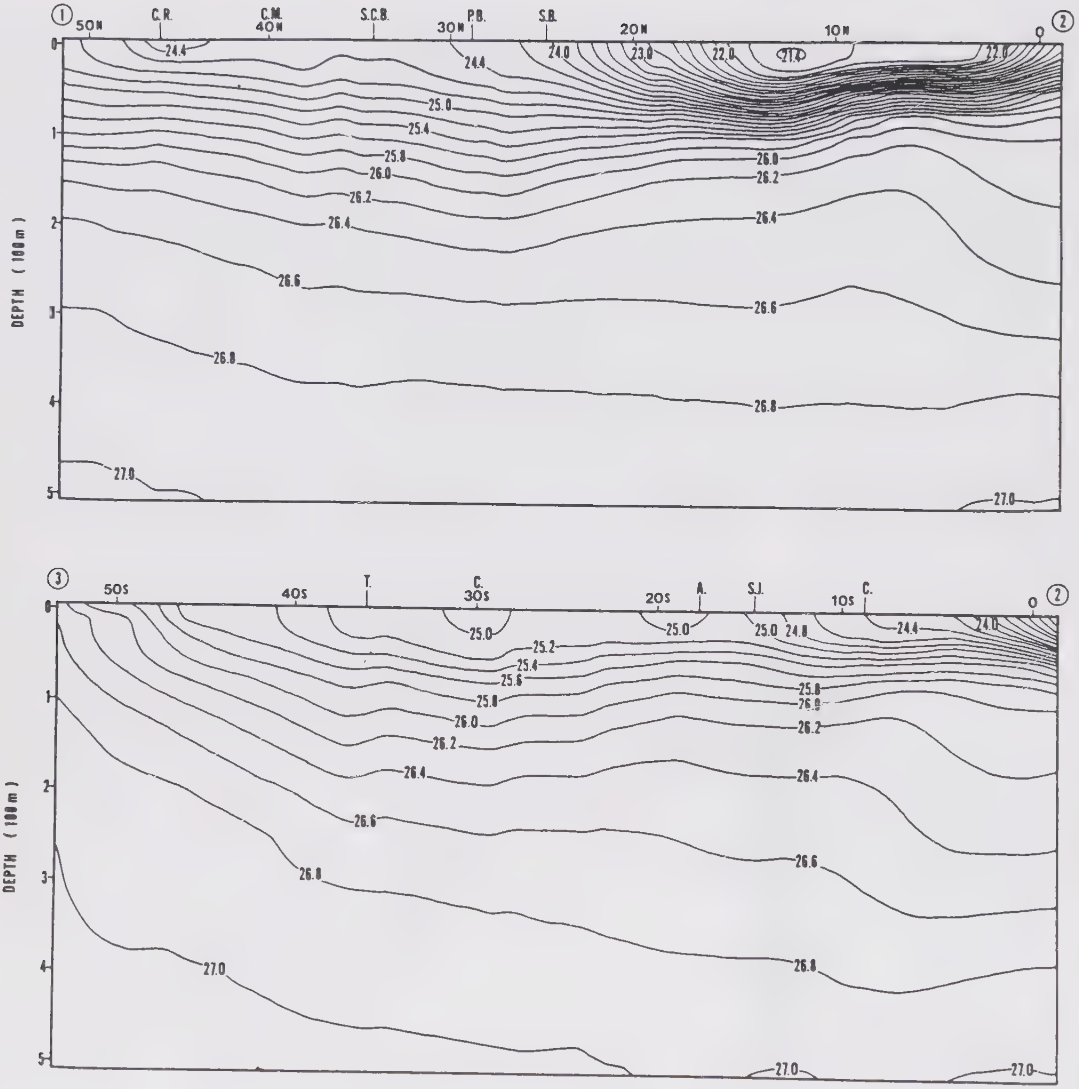

Figure 5. Sea water density (sigma-t) vs. depth along the eastern boundary of the Pacific Ocean. The orientation of the section is shown in Figure 1. Initials at the top of the diagram indicate the latitudinal positions of locations discussed in detail in Section III of this paper.

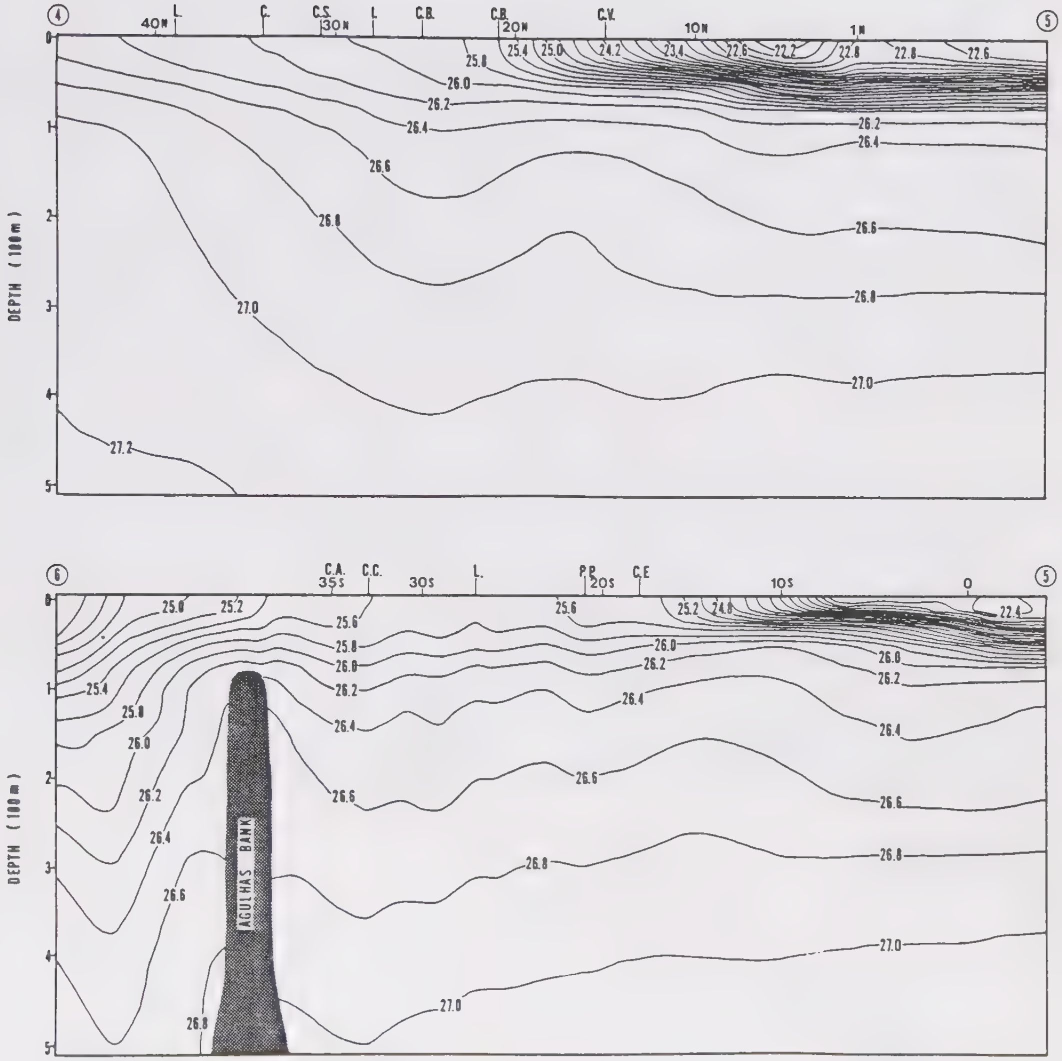

Figure 6. Sea water density (sigma-t) vs. depth along the eastern boundary of the Atlantic Ocean. The orientation of the section is shown in Figure 1. Lines at the top of the diagram indicate the latitudinal positions of locations discussed in detail in Section III of this paper.

SUBREGIONAL ASPECTS

The charts presented in the appendix are a subset of a considerable volume of material produced and examined in this study. In order to make "cuts" of this material for presentation we have chosen several fixed locations in each eastern boundary region which appear to exemplify the range of environmental characteristics encountered in the near-coastal environments. These locations are labeled in terms of a recognizable feature of coastal geography (i.e., a coastline feature or a coastal city) and appear on the appendix maps and on Figure 7, and are listed in Tables 2 to 6

Tables 2 and 3 briefly summarize information available on the geography and seasonality of sardine and anchovy spawning in the four eastern boundary current systems. The quality and quantity of information available varies widely among regions and within regions. Thus a fully consistent and complete synthesis is not available to us at this point. Tables 2 and 3 thus should not be considered to be "hard" data, and should not be cited as authority. They are presented as aids to recognition of patterns in the environmental summaries we have assembled (i.e., from the point of view of exploratory data analysis and hypothesis generation rather than of hypothesis testing). Our attempt at preliminary synthesis is intended to generate feedback from workshop participants and others with more specific knowledge of local situations. A discussion of the background and references to Tables 2 and 3 for the California and Peru systems are available in Bakun and Parrish (1982); major references for the Canary system are Bravo de Laguna, Fernandez, and Santana (1976), FAO (1978), and Belvèze and Bravo de Laguna (1980); major references for the Benguela system are King (1977), LeClus (1979), Badenhorst and Boyd (1980), Crawford (1980), and Crawford, Shelton, and Hutchings (1980).

Table 4 lists characteristic sea surface temperature values for 2-month segments of the annual cycle. These values were selected from bimonthly maps of long-term mean summaries which are described in the Appendix and from similar displays of the standard errors of the estimated mean values, in such a way as to characterize the shoreward 50 km of ocean or the locality over which spawning occurs. For example, in the Columbia River Plume, spawning occurs at distances of 100 km or more from the coast and so our presentations attempt to reflect conditions at that location, rather than directly adjacent to the coast.

Figure 7 displays the offshore component of surface Ekman transport plotted against the cube of the wind speed (indicating the rate of addition of turbulent mixing energy to the water column). Table 5 lists values of mixed layer depth obtained from bathythermograph data (Husby and Nelson, 1982). Sparsity of available data restricts this presentation to the California Current locations and the three northern locations in the Peru Current region. Profiles of stability structure for three Benguela locations based on hydrographic data, which lack the vertical resolution provided by bathythermograph traces, are shown in Figure 8. Table 6 contains the widths of the adjacent continental shelves.

Table 2. Spawning seasons of Pilchards
(Relative size of dots is only meaningful at each location)

	JAN-FEB	MAR-APR	MAY-JUN	JUL-AUG	SEP-OCT	NOV-DEC
COLUMBIA R.			•	•		
CAPE MENDOCINO						
S. CALIF. BIGHT	•	⬤	⬤	•		
PUNTA BAJA						
S. BAJA CALIF.	•	●	●	•	•	•

	JAN-FEB	MAR-APR	MAY-JUN	JUL-AUG	SEP-OCT	NOV-DEC
LISBON						
CASABLANCA	⬤	•	●	•	•	⬤
CAP SIM						
IFNI	⬤	•	●			⬤
C. BOJADOR						
CAP BLANC						
CAP VERT						

	JUL-AUG	SEP-OCT	NOV-DEC	JAN-FEB	MAR-APR	MAY-JUN
CHIMBOTE	⬤	●	•	•		
SAN JUAN						
ARICA	⬤	●	•	•	•	
COQUIMBO						
TALCAHUANO						
46°S						

	JUL-AUG	SEP-OCT	NOV-DEC	JAN-FEB	MAR-APR	MAY-JUN
CAP FRIO						
PALGRAVE PT.		●	•	⬤		
LUDERITZ						
C. COLUMBINE		●	●	⬤		
C. AGULHAS		●	●	⬤		

Table 3. Spawning seasons of Anchovies
(Relative size of dots is only meaningful at each location)

	JAN-FEB	MAR-APR	MAY-JUN	JUL-AUG	SEP-OCT	NOV-DEC
COLUMBIA R.			•	⬤		
CAPE MENDOCINO						
S. CALIF. BIGHT	⬤	⬤	•	•	•	•
PUNTA BAJA						
S. BAJA CALIF.	⬤	●	•	•	•	•

	JAN-FEB	MAR-APR	MAY-JUN	JUL-AUG	SEP-OCT	NOV-DEC
LISBON						
CASABLANCA						
CAP SIM						
IFNI						
C. BOJADOR			NO DATA			
CAP BLANC						
CAP VERT						

	JUL-AUG	SEP-OCT	NOV-DEC	JAN-FEB	MAR-APR	MAY-JUN
CHIMBOTE	●	⬤	•	•	•	•
SAN JUAN	●	●	•			
ARICA	⬤	●	•	•	•	•
COQUIMBO						
TALCAHUANO	●	•			•	⬤
46°S						

	JUL-AUG	SEP-OCT	NOV-DEC	JAN-FEB	MAR-APR	MAY-JUN
CAP FRIO						
PALGRAVE PT.		•	●	⬤	●	
LUDERITZ						
C. COLUMBINE						
C. AGULHAS		●	⬤	●		

Table 4. Sea Surface Temperature (°C)

	JAN-FEB	MAR-APR	MAY-JUN	JUL-AUG	SEP-OCT	NOV-DEC
COLUMBIA R.	9.2	9.5	12.6	15.1	14.7	11.3
CAPE MENDOCINO	11.0	10.6	11.1	12.1	12.9	12.1
S. CALIF. BIGHT	14.0	14.0	16.0	18.0	18.0	15.4
PUNTA BAJA	16.2	15.5	16.4	19.1	19.5	17.6
S. BAJA CALIF.	18.9	17.2	17.3	21.4	24.0	21.4

	JAN-FEB	MAR-APR	MAY-JUN	JUL-AUG	SEP-OCT	NOV-DEC
LISBON	14.0	14.0	16.2	18.0	18.0	15.2
CASABLANCA	16.4	16.5	18.8	22.3	21.6	18.1
CAP SIM	16.6	16.9	17.9	18.0	18.7	17.4
IFNI	17.1	17.6	18.2	19.8	20.0	18.4
C. BOJADOR	18.1	17.6	19.0	20.5	20.9	20.2
CAP BLANC	17.7	17.8	18.2	20.6	21.0	19.1
CAP VERT	19.6	19.5	23.0	27.2	27.8	24.5

	JUL-AUG	SEP-OCT	NOV-DEC	JAN-FEB	MAR-APR	MAY-JUN
CHIMBOTE	17.6	16.9	18.5	21.3	21.1	18.6
SAN JUAN	15.6	15.1	17.3	19.6	18.1	16.7
ARICA	16.8	17.6	20.3	22.9	21.8	18.9
COQUIMBO	13.6	13.5	15.3	17.1	16.5	14.5
TALCAHUANO	12.0	12.2	14.1	14.9	14.7	13.2
46°S	8.6	10.8	11.1	13.1	12.7	9.9

	JUL-AUG	SEP-OCT	NOV-DEC	JAN-FEB	MAR-APR	MAY-JUN
CAP FRIO	14.8	14.9	16.5	18.7	17.3	15.7
PALGRAVE PT.	14.8	14.2	15.0	18.6	17.6	16.1
LUDERITZ	13.0	13.0	14.0	15.0	14.0	14.5
C. COLUMBINE	14.0	14.7	16.0	16.0	15.0	15.0
C. AGULHAS	15.2	15.8	19.0	20.0	18.4	16.6

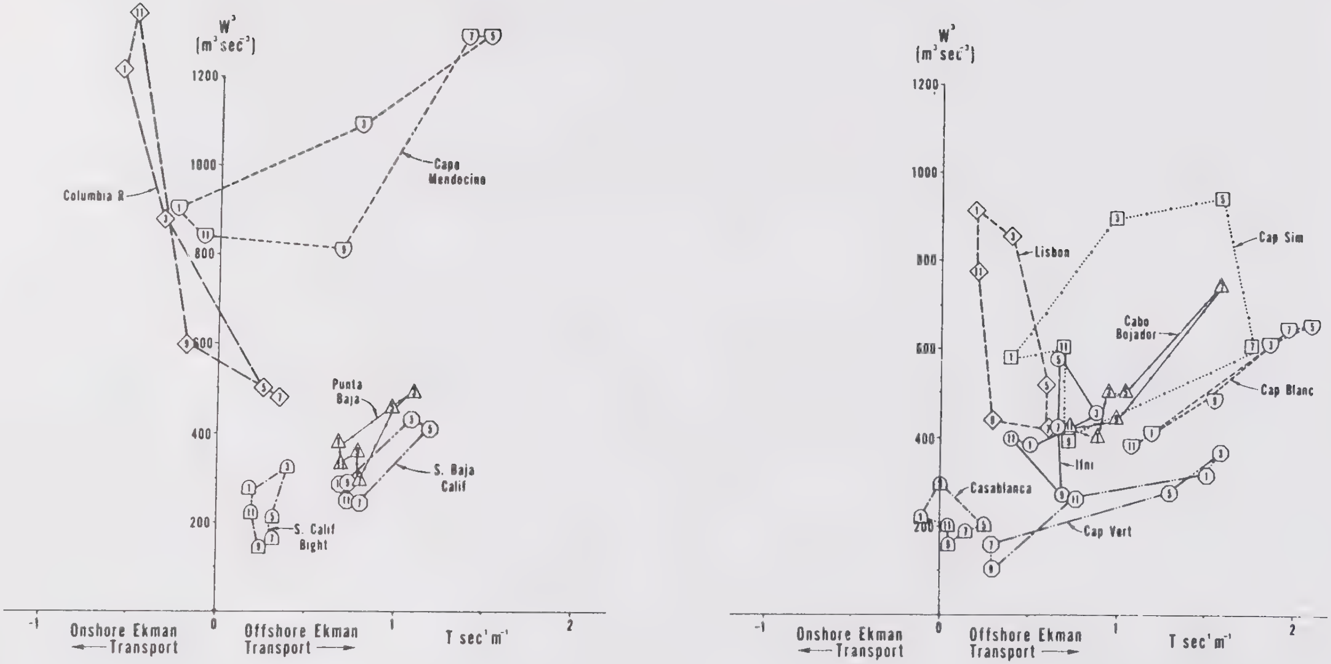

Figure 7. Characteristic seasonal relationships between W^3 (cube of the wind speed) index of turbulent mixing energy production and offshore Ekman transport at various locations in the California, Canary, Peru and Benguela Current systems. Each numbered symbol represents a 2-month climatological sample, with the number corresponding to the first month of the two (e.g., 1 represents Jan.-Feb., 3 represents Mar.-Apr., etc.).

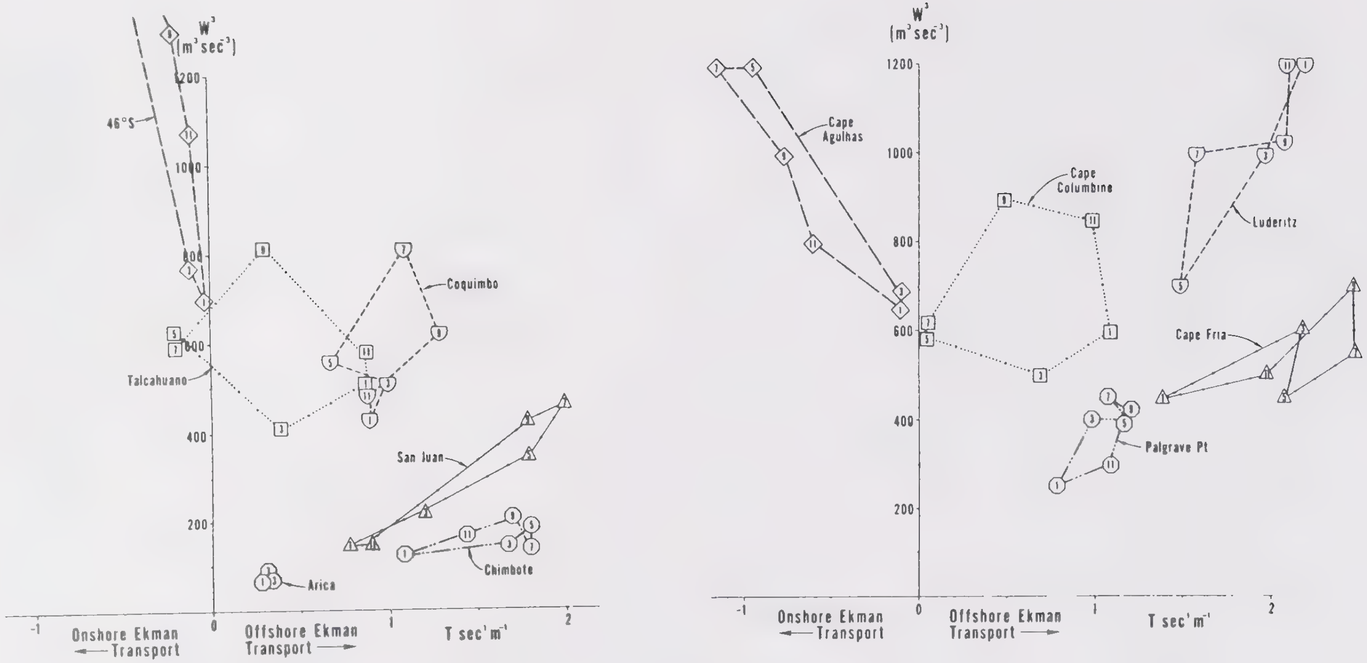

Figure 7. (continued)

Table 5. Mixed layer depths (meters) from historical bathythermograph records.

	JAN-FEB	MAR-APR	MAY-JUN	JUL-AUG	SEP-OCT	NOV-DEC
COLUMBIA R.	103	118	10	10	16	43
CAPE MENDOCINO	-	91	42	28	54	27
S. CALIF. BIGHT	37	25	11	10	14	20
PUNTA BAJA	37	26	18	12	14	26
S. BAJA CALIF.	45	23	18	9	20	34

	JUL-AUG	SEP-OCT	NOV-DEC	JAN-FEB	MAR-APR	MAY-JUN
CHIMBOTE	40	23	12	7	12	29
SAN JUAN	89	87	19	29	20	73
ARICA	14	18	9	5	5	10

Table 6. Approximate width* of continental shelf (km)

COLUMBIA R.	54	LISBON	43
CAPE MENDOCINO	21	CASABLANCA	56
S. CALIF. BIGHT	168	CAP SIM	38
PUNTA BAJA	29	IFNI	39
S. BAJA CALIF.	71	C. BOJADOR	40
		CAP BLANC	62
		CAP VERT	32

CHIMBOTE	132	CAPE FRIO	32
SAN JUAN	21	PALGRAVE PT.	73
ARICA	53	LUDERITZ	40
COQUIMBO	10	C. COLUMBINE	75
TALCAHUANO	44	C. AGULHAS	128
46°S	93		

*Distance from coast to 200-m contour (in the case of S. Calif. Bight, distance is to the 200-m contour at the seaward edge of the continental borderland).

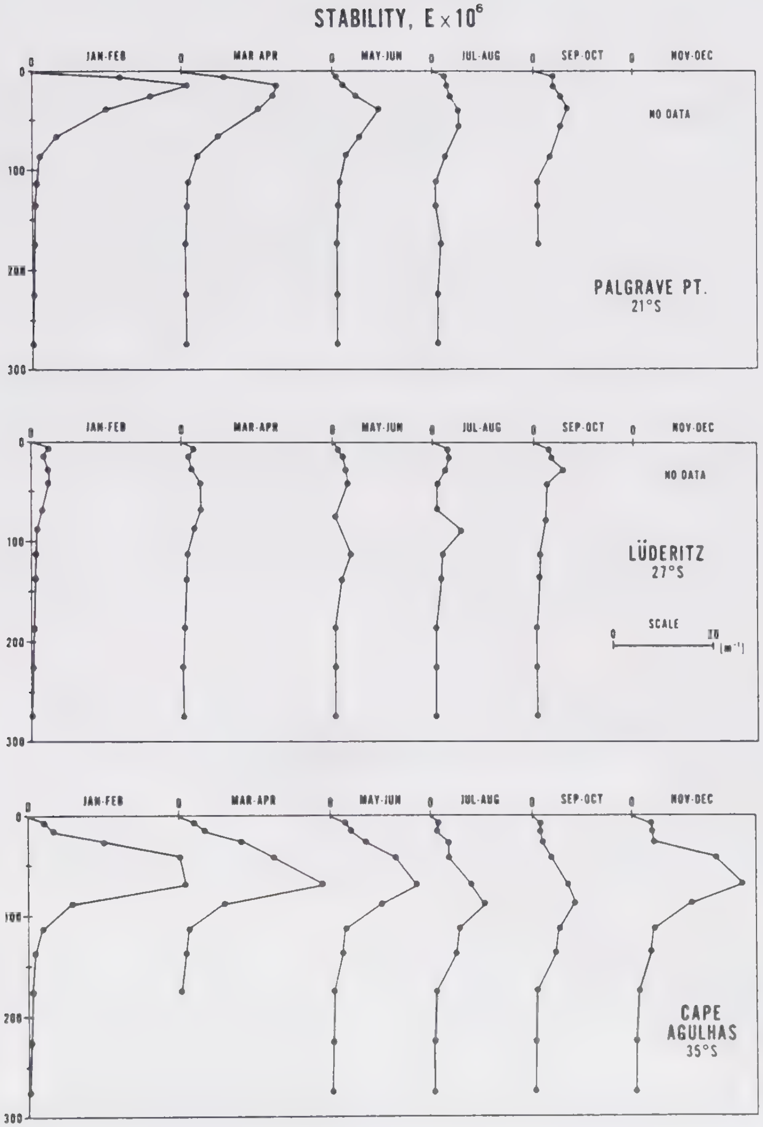

Figure 8. Static stability (m^{-1}) vs. depth for 2-month segments (for which there are sufficient hydrographic data to assemble a representative profile) of the seasonal cycles at three locations in the Benguela Current region. Depths are in meters. A scale for magnitude of stability appears to the right on the middle panel.

From these sources and the Appendix maps, the following compressed summary was constructed.

CALIFORNIA CURRENT SYSTEM

Columbia River. Anchovy spawning region (only in summer, moderate biomass); moderate continental shelf width; intense wind-generated turbulent mixing, relaxing during summer; stable upper ocean structure during summer due to lens of fresh water at the surface; onshore Ekman transport during winter--weak offshore Ekman transport during summer; little onshore-offshore temperature contrast except very near the coast.

Cape Mendocino. Primary upwelling center; narrow continental shelf; intense offshore Ekman transport, except in winter; intense turbulent mixing throughout the year; intense summer cold coastal temperature anomaly; small biomass of locally spawning fish populations; feeding grounds of adult pelagic fishes spawning elsewhere.

Southern California Bight. The major spawning grounds of pelagic fishes of the California Current; anchovy spawning region (entire year, peaking in winter-spring; large biomass); sardine spawning region (spring, pre-collapse landings 800,000 t); weak offshore Ekman transport; wide continental shelf; moderately weak turbulent mixing; relatively stable upper ocean density structure; warm coastal temperature anomalies extending very near to coast; semi-enclosed inshore gyral circulation pattern.

Punta Baja. Secondary upwelling center; narrow continental shelf; strong offshore Ekman transport, peaking in spring; moderate wind-generated turbulence; lies between two gyral circulations to the north and south and divides areas occupied by separate subpopulations of pelagic fishes. Some spawning occurs (often regarded as contiguous with Southern California Bight spawning populations). Weak negative coastal temperature anomaly.

Southern Baja California. Anchovy spawning region (winter-spring peak, moderate biomass); sardine spawning region (entire year, spring peak--moderate biomass); moderate continental shelf width; strong offshore Ekman transport; weak to moderate turbulent mixing; relatively stable upper ocean density structure; tendency for gyral circulation pattern; warm coastal temperature anomaly.

PERU CURRENT SYSTEM

Chimbote. Anchovy spawning region (spring peak, very large pre-collapse biomass); sardine spawning region (winter-spring); wide continental shelf; strong offshore Ekman transport and upwelling; weak wind-generated turbulence; very intense coastal cooling.

San Juan. Upwelling center; intense offshore Ekman transport, particularly in winter; narrow continental shelf; Turbulence level is low in summer, moderate in winter. Less stable stratification than in adjoining areas; very intense coastal cooling; reduced spawning of pelagic fishes relative to neighboring coastal areas (anchovy spawning appears to be intermediate in timing between Chimbote and Arica).

Arica. Anchovy spawning area (winter peak, large pre-collapse biomass); sardine spawning region (winter peak, large biomass); very low turbulence; weak offshore Ekman transport; moderate shelf width; extensive warm coastal temperature anomaly with a narrow band of cooling directly adjacent to the coast; gyral coastal circulation pattern.

Coquimbo. Upwelling center; intense offshore Ekman transport; extremely narrow continental shelf; cold coastal temperature anomalies extending hundreds of kilometers offshore. Turbulence level is moderate in summer, high in winter. No reported pelagic fish spawning.

Talcahuano. Seasonal upwelling (summer); moderate continental shelf width; turbulence level highest in spring; definite spatial minimum in fall and winter turbulence distributions. Anchovy spawning is reported (fall and winter only). Sardine eggs have been found.

46°S. Extreme wind-generated turbulent mixing--much higher than at the same latitude in the California Current region; no reported anchovy or sardine spawning.

CANARY CURRENT SYSTEM

Lisbon. Moderate upwelling; moderate to high wind-generated turbulence; moderately cool coastal temperature anomaly; moderate continental shelf width.

Casablanca. Sardine spawning region (peak in winter; secondary peak in summer); low turbulence levels (maximum in spring); low Ekman transport; moderate continental shelf width; slightly warm coastal temperature anomaly.

Cap Sim. Upwelling center (strongest offshore Ekman transport in summer); high wind-generated turbulence (minimum in fall); cold coastal temperature anomaly (intense in summer).

Ifni. Sardine spawning region (peak in winter, secondary peak in summer); moderate offshore Ekman transport (strongest in summer); moderate continental shelf width--shelf widens to the immediate south; local minimum in wind generated turbulence.

Cabo Bojador. Strong summer offshore Ekman transport--moderate offshore transport during the remainder of the year; fairly narrow continental shelf; turbulence levels moderate to high (summer maximum); substantial cold coastal temperature anomaly.

Cap Blanc. Upwelling center (intense offshore Ekman transport throughout the year); moderate continental shelf width; strong negative coastal temperature anomaly; moderate turbulent mixing in winter--stronger in summer.

Cap Vert. Highly seasonal upwelling; strong offshore Ekman transport in winter, relaxing greatly in summer; turbulence levels low in late summer and in fall--high in winter and spring; cold coastal temperature anomaly in winter--warm anomaly in summer. Summer and fall temperatures exceed 27°C.

BENGUELA CURRENT SYSTEM

Cape Frio. Upwelling center; intense offshore Ekman transport throughout the year, extreme in winter to early spring; strong coastal temperature gradients.

Palgrave Point. Anchovy and sardine spawning grounds (summer); substantial offshore Ekman transport (although much weaker than in the adjacent regions to the north and south--weakest in the summer); fairly wide continental shelf; weak to moderate turbulent mixing--weakest in summer (definite local minimum in the spatial distributions of wind-generated mixing energy production); stable density structure in summer.

Lüderitz. Upwelling center; very intense offshore Ekman transport; moderately narrow continental shelf; intense turbulent mixing--peak intensity in summer; intense cold coastal temperature anomaly throughout the year; low stability in the water column.

Cape Columbine. Sardine spawning grounds (summer--some anchovy spawning); seasonal upwelling; strong offshore Ekman transport in summer, vanishing in winter; moderate continental shelf width; moderate to strong turbulent mixing (spring maximum, fall minimum). A local minimum of turbulent mixing energy production lies within the coastal indentation just to the north of the cape.

Cape Agulhas. Anchovy and sardine spawning grounds (spring-summer); onshore Ekman transport; wide continental shelf; intense turbulent mixing, moderating somewhat in summer; stable ocean structure resulting from a thin lens of warm clear surface water from the Indian Ocean which overlies denser, more productive waters at depth (50-75 m).

PATTERN RECOGNITION

Our analyses of the climatological fields and information on spawning grounds suggest the following patterns. Upwelling centers, characterized by strong offshore Ekman transport, intense wind-generated turbulent mixing, reduced water column stability, and narrow continental shelves appear to be areas in which anchovies and sardines do not spawn. Spawning grounds tend to lie in coastal indentations where wind induced transport and turbulence are reduced and continental shelf width tends to be greater. The spawning grounds of the largest populations tend to be located downstream (equatorward) of upwelling centers. Smaller populations (e.g., Columbia River, Talcahuano) are located at the poleward extreme of upwelling regions where the upwelling is highly seasonal, and spawning occurs when various circumstances may reduce the effects of offshore transport and of mixing of the surface layers by the wind.

Temperature

Sea surface temperature is a better index for establishing cold temperature tolerance than warm temperature tolerance (i.e., it is a good index of the warmest water available but colder water is always available at greater depths). The physiological response of pilchard and anchovy eggs and larvae are best known for the stocks which spawn in the Southern California Bight. Lasker (1964) has shown that pilchard eggs and larvae developed normally between 13° and 21°C; however, larval mortality increased in experiments below 14°C. Incubation time decreased with increasing temperature and early growth was greatest at 16°-17°C. Anchovy eggs and larvae developed normally at 11°C (Lasker, 1964) and early growth was greatest at 21°C in the laboratory (Kramer and Zweifel, 1970).

As long as it does not approach the physiological limits, ambient temperature, at least in so far as it is reflected in sea surface temperature distributions (Table 4 and Appendix Charts 3 and 4), does not appear to exert any obvious control on reproductive habits. For example, seasonal spawning peaks off Southern Baja California and Cape Agulhas correspond to bimonthly temperature values of nearly 19°C, while at Talcahuano peak anchovy spawning occurs in winter at 13°C, even though warmer conditions are available at other seasons. Certainly, temperature conditions exceeding physiological tolerances would preclude occurrence. For example, it is probable that no anchovy spawning would occur in winter off the Columbia River (i.e., at 9°C) even if other conditions were favorable. However, in the regions where the temperatures are within physiological limits, the particular temperature appears not to be a dominant factor in determining spawning habits.

Turbulence

Spawning rarely occurs in areas of strong turbulent mixing of the upper water column. Spawning grounds are characterized by weak to moderate values of the mean cube of the wind speed, which is an index of the rate of addition of wind-generated turbulent energy to the water column (Husby and Nelson, 1982). Spawning grounds generally lie directly within spatial minima in the W^3 (wind speed cubed) distributions (Appendix Charts 9 and 10). Spawning habitats are characterized by increased stability in the internal density structure of the upper water column (Table 5, Fig. 8) that would resist dispersion of fine-scale food strata by turbulence events related to storms.

Where spawning grounds occur in regions of moderate wind-generated turbulence, other factors influencing stability may be favorable to spawning. For example, off the Columbia River the anchovy population spawns only in the summer (i.e., directly out of phase with other California Current anchovy populations). At this season, the W^3 index falls to moderate values (Fig. 7) and the subsurface stability is enhanced by the thin lens of less dense Columbia River Plume water at the sea surface. At Talcahuano, where turbulence conditions are not greatly lessened during summer, anchovy spawning remains generally in phase with other Peru Current populations; reference to Appendix Charts 9 and 10 will show that turbulent mixing in coastal areas north of Talcahuano is actually less in the winter downwelling season than in the summer upwelling season. Off Cape Agulhas, both anchovy and pilchard populations spawn under conditions characterized by substantial wind-generated mixing. However, this is a situation where particularly strong internal water column stability builds during the summer spawning season (Fig. 8), which may be due to an influx of warm Indian Ocean surface water (Darbyshire, 1966).

Transport

Areas of intense offshore transport conditions, where reproductive products might be lost from the vicinity of the coast, are characterized by minimum spawning of anchovies and pilchards. In many cases, the effects of transport and turbulence are confounded since strong wind driven offshore transport and strong wind-generated turbulence tend to coincide in eastern boundary upwelling systems. However, adaptations which result in the avoidance of offshore loss of reproductive products appear to be very widespread in fish species successfully inhabiting the California Current region (Parrish et al., 1981), indicating that transport must exact an important control on reproductive success. Note that in two situations where spawning takes place under relatively strong turbulent conditions (i.e., Talcahuano and Cape Agulhas) surface Ekman transport is directed onshore. In addition, Shelton and Hutchings (1982) have shown that a coastal jet between Cape Agulhas and Cape Columbine aids transport of larvae from the spawning grounds to the inshore nursery grounds. At Chimbote an enormous anchovy population has spawned in a situation characterized by strong offshore transport (Fig. 7); this situation is discussed in detail below.

DISCUSSION

The information presented in this analysis suggests that temperature, transport, and turbulence patterns greatly influence the timing and location of spawning grounds of anchovies and pilchards in eastern boundary currents. Furthermore no single feature has overriding control. It appears that individual stocks have adapted their reproductive strategies to achieve local optimum solutions to these three physical factors. We assume that this also applies to the three factors of the IREX equation which we have not addressed: food, predation, and population density. The question of how good individual optimum solutions are, is probably best judged by the size of the stocks.

The four major eastern boundary currents have a great deal in common. The locations and seasonality of maximum offshore Ekman transport appear to be closely related to the seasonal latitudinal shifts of the atmospheric pressure systems, intensification of the large-scale pressure gradients, and the relationships between these systems and the large-scale topography of the continents. However, as can be seen in the environmental features presented here, there are also large differences among them. For example, all four systems have maximum cold inshore-offshore temperature anomalies associated with summer maxima of offshore Ekman transport. These summer "maximum upwelling regions" have anchovy and/or sardine stocks with spawning grounds poleward and equatorward of them. The California and Benguela systems each have a single area with cold sea surface temperature anomalies. In the California system this area is located in the summer upwelling maximum, whereas the Benguela system's area includes the summer upwelling maximum at Lüderitz and a winter upwelling maximum at Cape Frio. The Peru and Canary systems each have two separate areas of cold sea surface temperature anomalies. The Peru system has an area located at the winter upwelling maximum (San Juan to Chimbote) and a second area in the upwelling region off central Chile which has a summer maximum near Talcahuano. The Canary system has a summer upwelling maximum off Lisbon and a second summer upwelling maximum between Cap Sim and Cap Blanc. During the winter the cold water anomaly off northwest Africa shifts south and the upwelling maximum then extends from Cap Blanc to Cap Vert.

We have noted that spawning of anchovies and pilchards does not occur in the summer upwelling maximum regions, which are characterized by extensive offshore Ekman transport and high wind speed cubed values. Summer mean sea surface temperature values in these upwelling maxima vary from 12°C at Cape Mendocino to 18°C at Cap Sim and Lisbon. Spawning grounds and different stocks generally occur "upstream" and "downstream" of these summer maxima. This suggests that one way to classify the stocks is by their location with respect to upwelling maxima.

Our three classes would be (1) stocks poleward of the summer upwelling maxima, (2) stocks equatorward of the summer upwelling maxima, and (3) stocks equatorward of the winter upwelling maxima. Note that very little is known of the stocks in the lower latitudes of the Canary Current. This classification system also works reasonably well in describing potential fishery yields. Maximum annual yields observed in the higher latitude stocks range from 100,000 to 400,000 tons. Maximum yields in the second group are between 800,000 and 2,000,000 tons. The only stock in the third group, the Peruvian anchoveta, yielded in excess of 10,000,000 tons.

The stocks with spawning grounds equatorward of the summer upwelling maxima, with the exception of the stock spawning near Palgrave Point, have a number of features in common. Their spawning grounds (i.e., the Southern California Bight, Arica, Casablanca, and Ifni) are in bights with weak offshore Ekman transport, little inshore-offshore temperature anomaly, and low wind speed cubed values. The anchovy stocks tend to spawn in the late winter - early spring and peak pilchard spawning is either at the same time or just after the anchovy peak. The Palgrave Point spawning grounds occur within an area with a cold inshore-offshore temperature anomaly and spawning in this region occurs in summer when offshore transport and turbulence are at a local minimum. Mean sea surface temperature is in the 14°-18°C range during the spawning season in all of spawning grounds.

The higher latitude stocks (i.e., those with spawning grounds near the Columbia River, Talcahauno, and Cape Agulhas) are in areas in which turbulence (wind speed cubed) varies seasonally from moderate to high. We have not analyzed the high latitude region of the Canary Current. Ekman transport is onshore during the spawning season in the Talcahauno and Cape Agulhas spawning grounds. The Columbia River region has weak offshore transport during the spawning season and onshore transport during the rest of the year. The Columbia River and Cape Agulhas stocks spawn in the summer when wind speed cubed is at a minimum and spawning occurs in areas where the stability of the water column is increased by intrusions of different water masses (e.g., Columbia River water and Agulhas Current water). The Talcahauno anchoveta stock spawns in the early winter (Jordán, 1980) instead of in the summer when sea surface temperature is at a maximum. We do not know the exact location of this stock's spawning grounds, however, a region of minimum wind speed cubed lies just north of Talcahauno in the early winter.

THE PERUVIAN ANOMALY

The anchoveta stock, spawning in the area centered near Chimbote, has been by far the largest stock in the world. We have noted that this area stands out as an anomaly among the major spawning regions in that it is characterized by strong offshore Ekman transport (Fig. 7). Several factors could conceivably be acting to minimize associated offshore loss of reproductive products from this area.

Huyer (1976) has indicated that the offshore extent of coastal upwelling regions may be expanded in regions of wide continental shelves; the continental shelf off Chimbote is much wider than off other upwelling centers (Table 6). Also, the Rossby radius of deformation, which is the intrinsic coastal boundary layer width scale (Mooers and Allen, 1973), is inversely dependent on the sine of the latitude. Thus the Rossby radius at Chimbote (lat. 9°S) is about twice that at Arica, Palgrave Point, or Cap Blanc, more than 3 times that at Coquimbo, Punta Baja, or Ifni, and about 4 times that at Cape Mendocino or Lisbon.

A more speculative set of considerations concerns the dependence of Ekman layer depth on latitude. The expression for the Ekman depth scale (Ekman, 1905) contains the square root of the sine of the latitude in the denominator. Thus, for comparable vertical eddy viscosities, the Ekman depth at Chimbote would be twice that at Cape Mendocino or Lisbon, for example. For a given magnitude of offshore transport, therefore, the corresponding average offshore velocity of the Ekman layer off Chimbote would be one-half that off Cape Mendocino or Lisbon. Opposing this effect would be the expectation that increasing turbulence input at the higher latitude locations would tend to increase the vertical eddy viscosity which is in the numerator of the Ekman depth expression.

Bakun and Parrish (1982) noted that the peak spawning off Chimbote in winter occurs during the season of strongest offshore transport and hypothesized avoidance of detrimental effects of intermittent El Niño events as a possible reason. An alternate hypothesis concerns Ekman depth which tends to be limited by sharp density discontinuities due to inhibition of vertical eddy viscosity, such that the layer above the discontinuity tends to slide over the denser lower layer which will be relatively unaffected (Neumann and Pierson, 1966, p. 196). The mixed layer depth (Table 5) off Chimbote is much less (7 m) during summer than in winter (40 m). Averaging the corresponding summer (1.1 $m^2 sec^{-1}$) and winter (1.8 $m^2 sec^{-1}$) Ekman transports (Fig. 7) over these depth layers yields average offshore Ekman speeds of approximately 0.04 m sec^{-1} (3.5 km d^{-1}) in winter and 0.16 m sec^{-1} (14.0 km d^{-1}) in summer. Planktonic reproductive products within the mixed layer would thereby be dispersed offshore four times as rapidly during summer than during the winter spawning peak.

IMPLICATIONS FOR POPULATION MODELING

Fishery time series are generally quite short and often contain only one to several realizations of major shifts in trend (e.g., Fig. 2). The result is that there are often insufficient degrees of freedom for purely empirical approaches to be effective in defining relationships with multiple environmental factors. Thus it is important to incorporate as much accessory information as can be gleaned independently from the actual time series data. Accessory information can come from process-oriented experiments or from various deductive approaches such as the one we have presented in this paper.

The most straightforward way to incorporate this sort of information is in the choice and formulation of the explanatory variables. By choosing a very limited set of variables which addresses only those processes which appear to be the most crucial and by formulating these variables specifically according to the manner in which they appear to affect the populations, the degrees of freedom available in the time series can be expended with the greatest likelihood of generating beneficial information (Bakun and Parrish, 1980).

In this study we have compared seasonality and geography of reproduction with corresponding features in the environment. Since natural selection implies adaptation of reproductive strategies to the most crucial processes affecting reproductive success, patterns of correspondence may illuminate the environmental linkages.

We have noted that spawning tends not to occur in regions characterized by wind conditions which would generate intense turbulent mixing of the upper water column. This would tend to support Lasker's (1978) mechanism for larval mortality caused by wind-generated turbulent dispersion of fine-scale strata of food particles appropriate for first-feeding. Some degree of information on surface wind conditions is generally available. In view of the hypothesized mechanism, the average turbulence generation over monthly or longer intervals is probably not the ideal way to formulate this variable. Rather, the frequency and duration of periods where wind speeds do not exceed a critical threshold, above which it would breakdown the underlying water column stability, may be more pertinent considerations (Husby and Nelson, 1982). No specifics of such a formulation have been proposed.

Another pattern in reproductive strategies is the absence of spawning in regions characterized by strong offshore transport whereby reproductive products are lost. This mechanism tends to be confounded with the turbulence mechanism in the situations we are examining. For example, in upwelling centers, strong offshore transport coincides with intense turbulence generation. However, we have noted indications that the transport mechanism is acting (i.e., in certain situations where characteristic transport is not directed strongly offshore, spawning occurs under conditions which appear to by typified by substantial wind-generated turbulence). We have also speculated that the seasonality of spawning at Chimbote is tuned so as to minimize offshore dispersion of reproductive products, rather than to minimize turbulent mixing.

As is the case for the turbulence indices, estimates of offshore Ekman transport (e.g., Bakun, 1973) can also be generated from wind information. However, the two mechanisms imply distinctly different time scales. The turbulence mechanism acts to cause larval starvation on a time scale of a few days; it is non-linear in that water once mixed is not unmixed by reversing the action of the wind. The transport mechanism acts on much longer time scales and may indirectly cause mortality of late larvae and juveniles by displacing them from the favorable coastal environments. Transport is linearly additive; a period of offshore transport could be counteracted by a later period of onshore transport.

No pattern has emerged to indicate that reproductive strategies are strongly influenced by an optimum temperature. Obviously, the physiological temperature limits of the organisms provide barriers to reproduction in extreme cases. This analysis suggests that the effective way to incorporate temperature data in an empirical recruitment model may be simply as an indicator variable which has a value of "one" for a range of temperatures within which spawning can occur and "zero" beyond that range. An additional temperature effect, which may become significant once the variance due to the indicator variable is accounted for, may occur due to increases in physiological rates, etc., by increases in temperature within the generally favorable range.

APPENDIX

OCEANOGRAPHIC DATA

To assemble characteristic distributions of the large-scale oceanographic features in the four boundary current regions, we used existing global summaries of subsurface data. Objectively analyzed fields of annual mean temperature, salinity, and oxygen at standard depths were provided by Sydney Levitus of the National Oceanic and Atmospheric Administration's (NOAA) Geophysical Fluid Dynamics Laboratory (GFDL). Data sources and analysis methods and selected horizontal distributions and vertical sections are described in detail by Levitus and Oort (1977) and Levitus (1982).

The annual mean geostrophic flow at the surface was constructed from the analyzed fields of temperature and salinity defined on a grid of 1-degree latitude by 1-degree longitude in each of the eastern boundary current regions. Dynamic topographies relative to the 1000 db level (approximately 1000 m) were computed following LaFond (1951). The computation points for surface velocity are offset from the values of dynamic height by a half-degree in both directions (i.e., calculated velocities are centered on the whole degree of latitude and longitude). Therefore, a velocity vector for each 1-degree square was calculated from the gradients defined by dynamic height values at the corners of each square. To clarify the presentations shown in Chart 1, vector symbols are only plotted for alternate 1-degree squares in both latitude and longitude coordinates. Contours of dynamic height (in dynamic meters, with a contour interval of 0.04 dyn m) are superimposed on the vector fields as an aid to interpreting the flow direction and strength (i.e., the surface geostrophic flow is parallel to contours of dynamic height and the current speed is inversely proportional to the contour spacing and to the sine of the latitude). Directions are defined such that higher values of dynamic height lie to the right (left) of the current in the northern (southern) hemisphere when facing in the direction of flow.

The analyzed fields from which these velocity calculations have been made were designed for global, rather than regional studies of ocean circulation. Well recognized seasonal variations in surface current features are not depicted in the annual mean distributions. For example, where speeds represented in Chart 1 vary from 2 to 10 cm sec^{-1}, typical seasonal ranges may be up to an order of magnitude larger. The results are rather smooth representations in which much of the temporal and spatial detail available in finer scale summaries (Wyllie, 1966; Hart and Currie, 1960; Robles, 1979) has been filtered out. No attempt has been made to extrapolate the dynamic height calculations into shallow coastal regions (i.e., bottom depths less than 1000 m). Where these summaries do not depict major circulation features near the coast, the predominant flow directions have been indicated by shaded arrows (e.g., over the Agulhas Bank and in the Southern California Bight).

Characteristic vertical sections of oxygen (Figs. 3,4) and density (Figs. 5,6) along predominantly meridional axes of the eastern boundary current systems were also constructed from the large-scale analyses. The locations of the sections are shown in Figure 1. Although the sections lie up to several hundred kilometers from the coast, the general features (e.g., oxygen minima) are felt to be representative of the coastal regimes, as well. Values of oxygen (mL L^{-1}) defined at standard depths between the surface and 1500 m are contoured with an interval of 0.5 mL L^{-1}. Oxygen minima (values less than 1.0 mL L^{-1}) are indicated by cross-hatching. Analogous sections of density (sigma-t) were derived from the annual mean values of temperature and salinity in the upper 500 m of the water column. Values of sigma-t are contoured with an interval of 0.2. On each vertical section, the latitudinal locations associated with prominent coastal features (e.g., capes and coastal cities) are designated by simple letter abbreviations. The reader is directed to Figure 1 and to Chart 1 for proper orientation of each section.

Historical mechanical bathythermograph (MBT) profiles and hydrocast data (temperature and salinity versus depth) archived in the Master Oceanographic Observation Data Set (MOODS) at the U.S. Navy's Fleet Numerical Oceanography Center (FNOC) in Monterey, California were used to calculate indices of mixed layer depth (Table 5) and selected profiles of vertical stability (Fig. 8). Mixed layer depths (in meters) were defined and calculated as described by Husby and Nelson (1982). The vertical gradient of sigma-t was used as an index of the static stability (E) of the water column, as suggested by Hesselberg and Sverdrup (1915; cited in Sverdrup, Johnson, and Fleming, 1942). Bimonthly vertical profiles of static stability (E x 10^{6} m^{-1}) in the upper 300 m are displayed for three locations in the Benguela Current system (Fig. 8).

SURFACE MARINE DATA

The climatological distributions of sea surface temperature, coastal-oceanic temperature contrast, surface layer Ekman transport, wind-generated turbulent energy production, and total cloud amount presented in this appendix are based on summaries of data contained in the National Climatic Center's (NCC) file of surface marine observations (Tape Data Family-11). The total file contains in excess of 50 million individual ship reports dating from the mid-19th century through 1979. Over 3.3 million of the reports are from the area of the Canary Current system. Summaries for the California and Benguela Current regions are based on 1.9 million and 1 million individual reports, respectively. The area off western South America contains an order of magnitude fewer surface weather observations (0.3 million).

Long-term composite summer and winter distributions of surface atmospheric properties were compiled by 1-degree latitude and longitude quadrangles within the four geographical regions outlined in Figure 1. The boundaries of the summary grids are defined as follows:

1. California Current - extends from lat. 20° N to 50°N and from the coast to 15 degrees of longitude offshore.

2. Peru Current - extends from lat. 50° S to 4°S and from the coast to 14 degrees of longitude offshore.

3. Canary Current - extends from lat. 5° N to 45°N and from the coast to 15 degrees of longitude offshore.

4. Benguela Current - extends from lat. 39° S to 8° S and from long. 35° E to 2° E; off the southwest coast, the data extend from the coast to 11 degrees of longitude offshore.

In each case, the data grid parallels the coastline configuration and each 1-degree quadrilateral is centered on a whole degree of latitude and longitude. All observations available in the TDF-11 file within the summary regions were averaged over six, two-month periods. Therefore, a mean value for each two-month period and square is formed from a data set which is independent of all other months and squares. Although all six bimonthly distributions were examined, we selected the January-February and July-August fields to represent the characteristic distributions for summer and winter seasons in the respective hemispheres.

The observations contained in the TDF-11 file vary markedly in methods and precision of measurement due to the changes in instrumentation, sampling techniques, and reporting procedures over the considerable time period covered by the data base. Based on the documentation for the TDF-11 data file[4/], a single pass editor was used to remove gross errors in the data, including erroneous position reports, and observations of sea surface temperature, wind speed and direction, and cloud amount exceeding extreme value limits. Detailed discussions of the sources of measurement errors and techniques for more refined data editing may be found in Bakun, McLain, and Mayo (1974), Nelson (1977), and Nelson and Husby (1983).

The spatial distributions of surface marine observations are known to be biased to the coastwise and transoceanic shipping lanes between major seaports. Chart 2 shows the distribution of total numbers of observations per 1-degree quadrangle in each boundary current region. A contour interval of 5,000 has been used and values exceeding 10,000 observations per 1-degree square are shaded. However, note that for the Peru Current region, the contour interval is 500 and values greater than 1000 observations per 1-degree square are shaded. In most cases, the highest density of reports lies within 300 km of the coast, except off southwestern Africa, where the narrow main shipping lane diverges sharply from the coast north of Cape Columbine. The numbers of reports per 1-degree square range from fewer than 50 off Peru and Chile to more than 40,000 in the Southern California Bight and off the Iberian Peninsula. Summer and winter averages are most reliable within the well traveled shipping lanes, but less precise in the offshore regions. Some temporal bias may also exist, since approximately 60-80 percent of the total reports have been taken since 1950.

[4/] National Climatic Center, Tape Data Family 11, NOAA/EDIS/NCC, Asheville, N.C.

The composite distributions are based on independent 1-degree square sample means. Detail within a single square which is not supported by similar values in surrounding squares reflects sampling error. Therefore, when contoured fields have been used to display the results of this study, the mean distributions have been machine contoured, subjectively smoothed, and recontoured to remove extreme values which were not supported by data in directly adjacent squares. Typically, "bull's-eyes" in the contoured fields reflected a paucity of ship observations or inadequate sampling of extreme events.

Sea Surface Temperature- Charts 3 and 4

Summer and winter distributions of sea surface temperature (°C) are contoured at intervals of 1°C. Seasonal cycles of sea surface temperature at selected coastal locations in each boundary current are listed in Table 4.

Coastal Temperature Anomaly - Charts 5 and 6

Summer and winter distributions of coastal temperature anomaly were constructed from the corresponding fields of sea surface temperature as follows. A smoothed offshore temperature reference was constructed by successively applying, at each 1-degree latitude increment, a 5-degree latitude by 3-degree longitude moving-average filter centered at the tenth 1-degree square from the coast. Sampling irregularities were reduced by discarding the three highest and three lowest values of the fifteen sample averages covered by the filter at each step, and averaging the remaining nine values. The value of this offshore reference temperature at the proper latitude was subtracted from each 1-degree averaged sea surface temperature. The coastal temperature anomaly, therefore, is the difference between the sea surface temperature at each location and the large-scale temperature offshore. The method is similar to that used by Böhnecke (1936; cited in Wooster and Reid, 1963) to describe the Canary Current and Benguela Current upwelling systems, in that it attempts to filter the basin-wide meridional temperature gradient, thereby highlighting local effects.

Temperature anomalies (°C) are contoured with an interval of 1°C. Anomalies less than -2°C are shaded. Cross-hatching designates positive anomalies greater than 1°C. Negative anomalies indicate that the mean sea surface temperature is colder than the offshore reference temperature; positive values indicate the opposite.

Ekman Transport - Charts 7 and 8

Surface wind reports from the TDF-11 data file were used to construct summer and winter distributions of surface layer Ekman transport in each of the eastern boundary current regions. Ekman transport is calculated as the ratio of the wind stress magnitude to the local value of the Coriolis parameter, and is directed 90° to the right (left) of the surface wind stress in the northern (southern) hemisphere. The method of calculation is described by Bakun et al. (1974). To clarify the presentations, vector symbols are only plotted for alternate 1-degree squares in both latitude and longitude coordinates. Ekman transport is plotted in units of metric tons per second per meter ($t\ sec^{-1}\ m^{-1}$), and vector symbols are scaled according to the key on the charts.

Scatter diagrams of Ekman transport versus the cube of the wind speed (Fig. 7) are used to distinguish between regimes characterized by strong surface layer transport and those dominated by wind-generated turbulence. At selected locations along each coast, vector means were resolved into components perpendicular and parallel to the coast. Coastline angles were determined by visually fitting a line to the dominant trend of the coast. Estimates of the offshore (onshore) directed component of Ekman transport are plotted against the cube of the wind speed in Figure 7.

Wind Speed Cubed - Charts 9 and 10

The rate at which turbulent kinetic energy of the wind is added to the upper ocean and becomes available to mix the stable thermocline layers is proportional to the third power, or "cube" of the wind speed (Niiler and Kraus, 1977). Mean summer and winter distributions of the cube of the surface wind speed were compiled from the TDF-11 surface wind reports following the methods of Husby and Nelson (1982). Mean values are plotted in units of 1000 m^3 sec^{-3} and contoured with an interval of 250 m^3 sec^{-3}. One-degree means of wind speed cubed at selected locations in each boundary current are plotted against offshore (onshore) Ekman transport in Figure 7.

Total Cloud Amount - Charts 11 and 12

Mean distributions of total cloud amount were assembled from the TDF-11 data file following procedures modified from Nelson and Husby (1983). Mean values are plotted in units of tenths of sky obscured and the contour interval is one-tenth. Based on the general patterns of cloud cover, certain inferences may be made about the expected distributions of net insolation. In particular, it should be noted that the summer distributions (Chart 11) show relative cloud cover minima at coastal locations characterized as centers of upwelling (e.g., Cape Mendocino, Cap Blanc to Cabo Bojador, Talcahuano, and Cape Columbine to Lüderitz). One implication of these distributions is that higher levels of incoming shortwave radiation reach the sea surface in the highly productive upwelling regions than elsewhere in the eastern boundary current systems (Bakun and Nelson, 1977; Nelson and Husby, 1983).

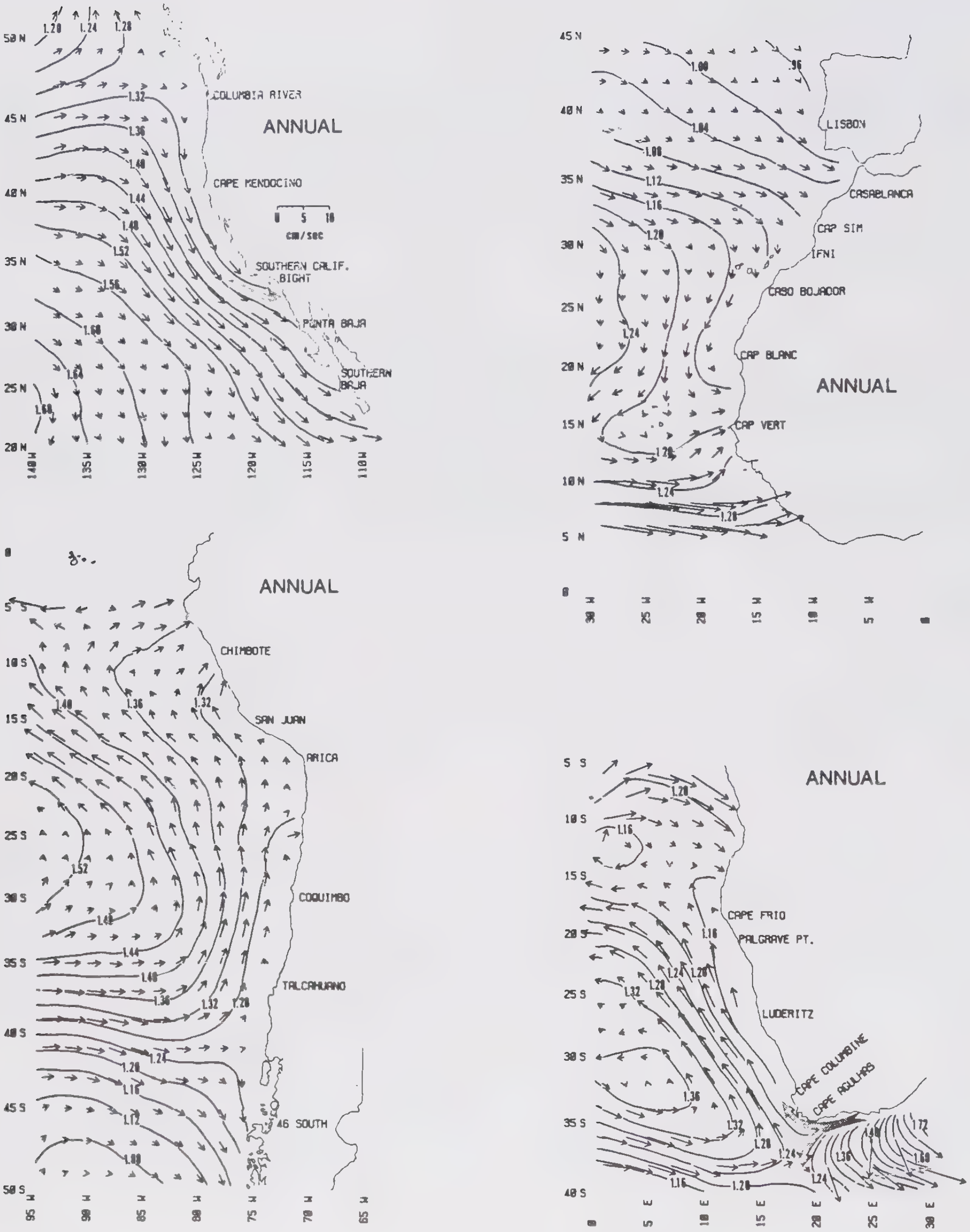

Chart I. Annual mean surface geostrophic flow (0/1000 db, cm sec^{-1}) and dynamic topography (dyn m).

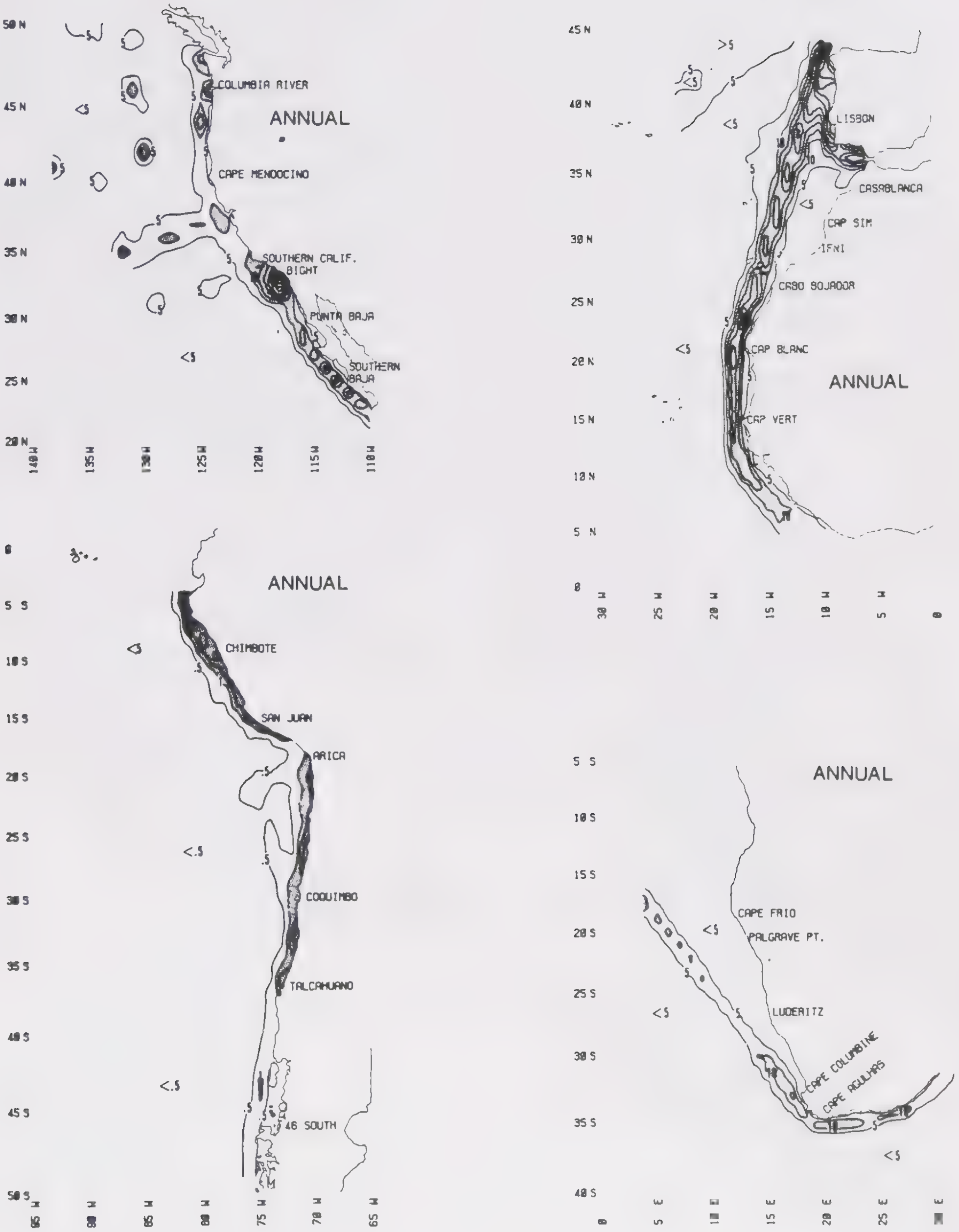

Chart 2. Distributions of observations per 1-degree square (thousands of observations)

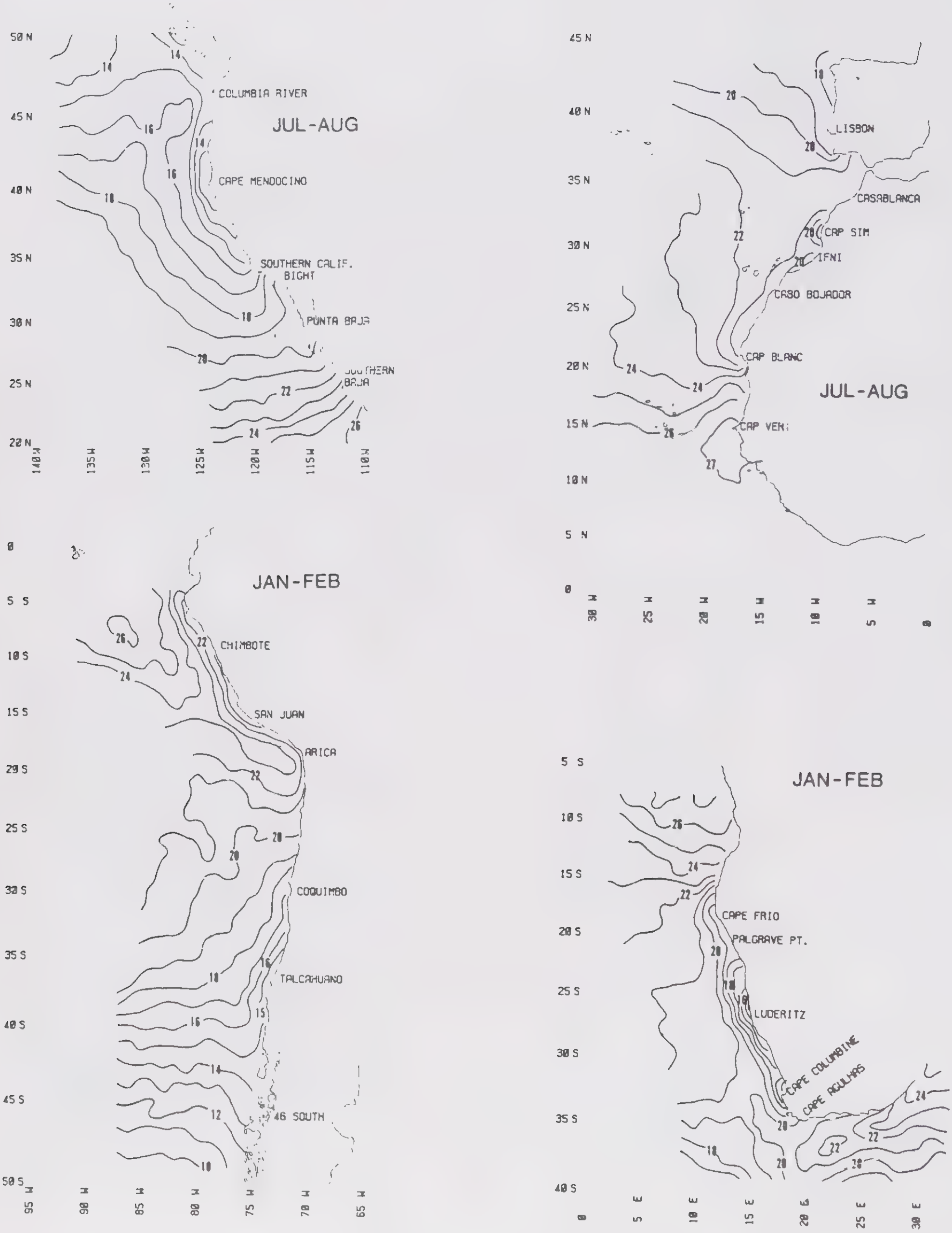

Chart 3. Summer sea surface temperature (°C).

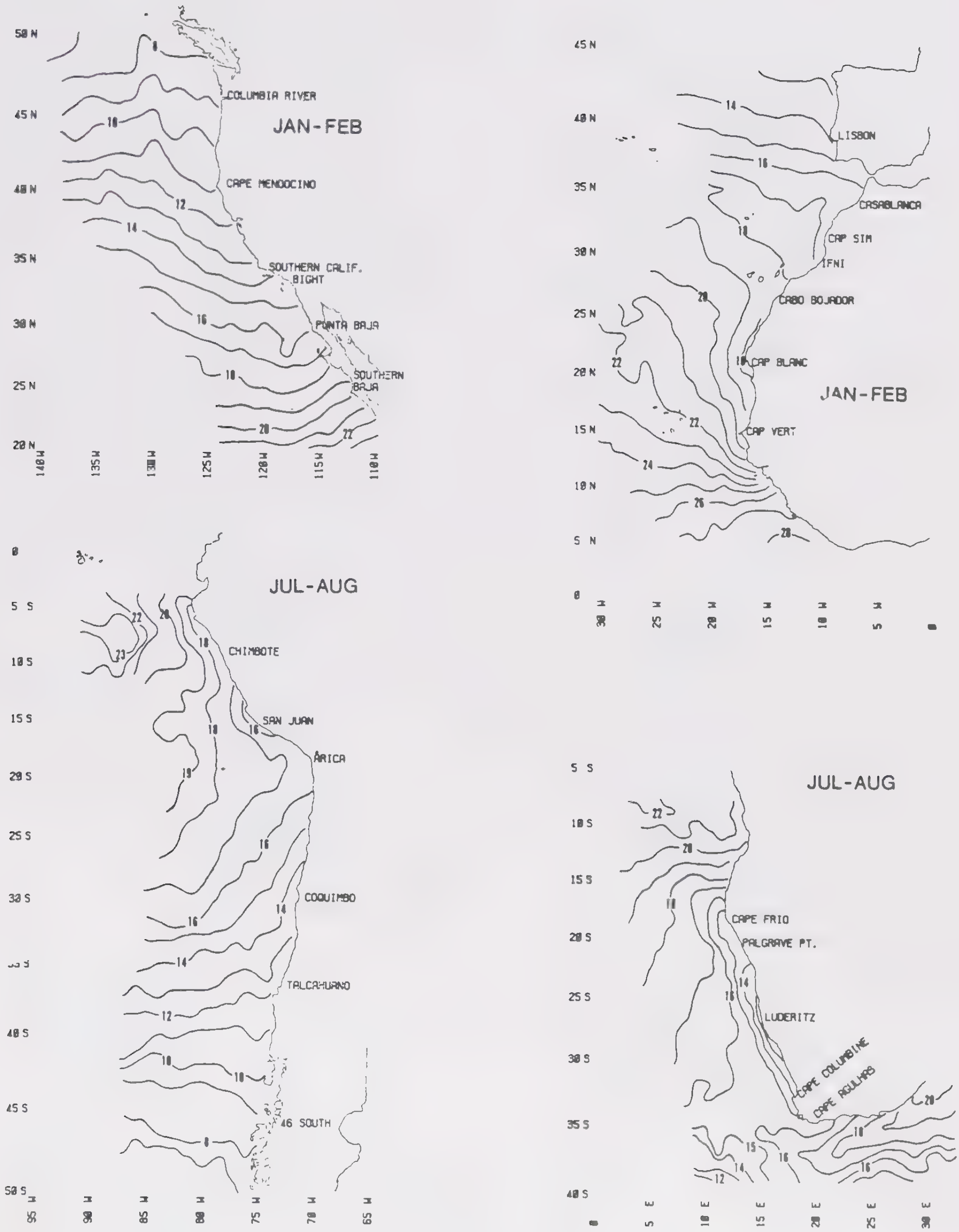

Chart 4. Winter sea surface temperature (°C).

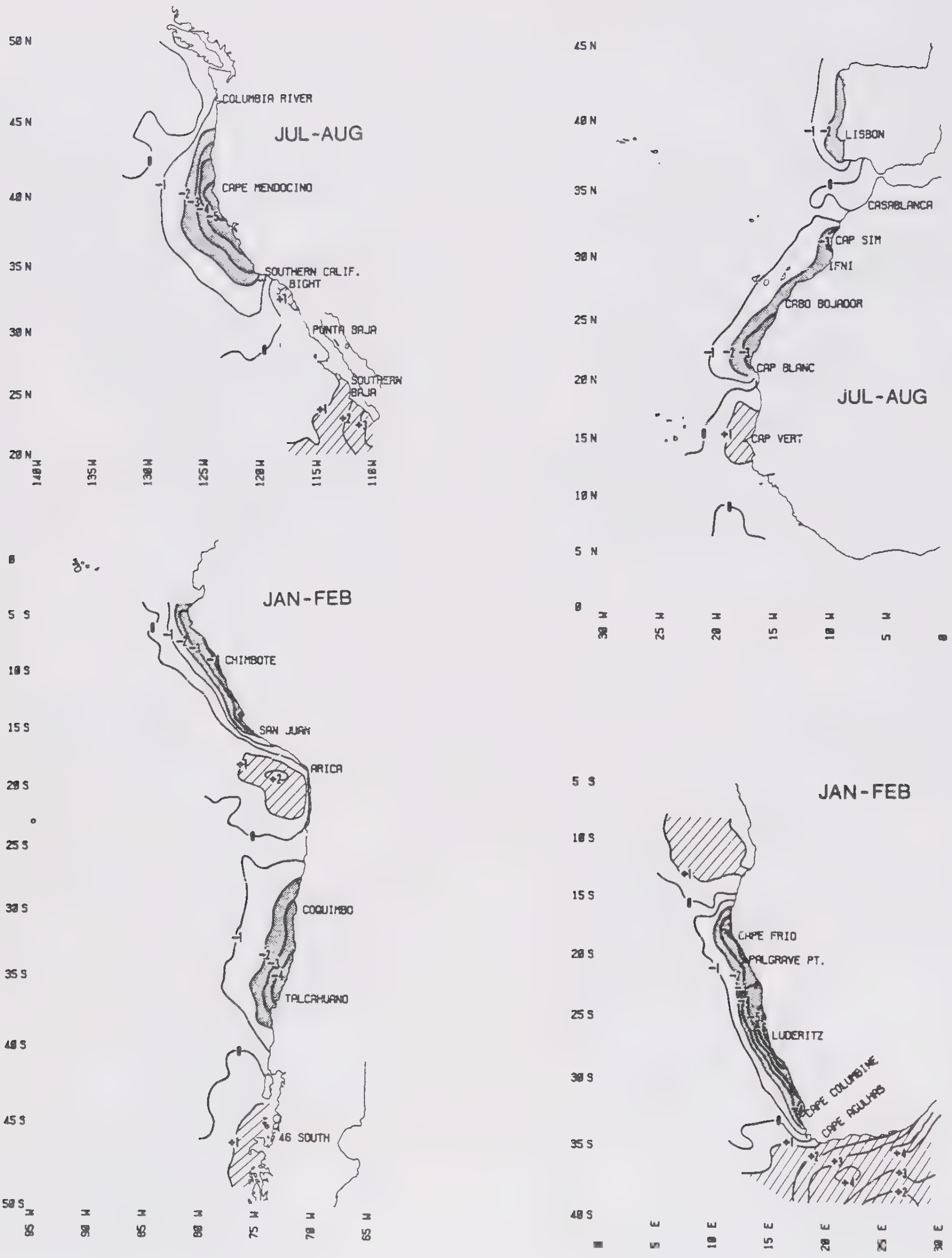

Chart 5. Summer coastal sea surface temperature anomaly (°C).

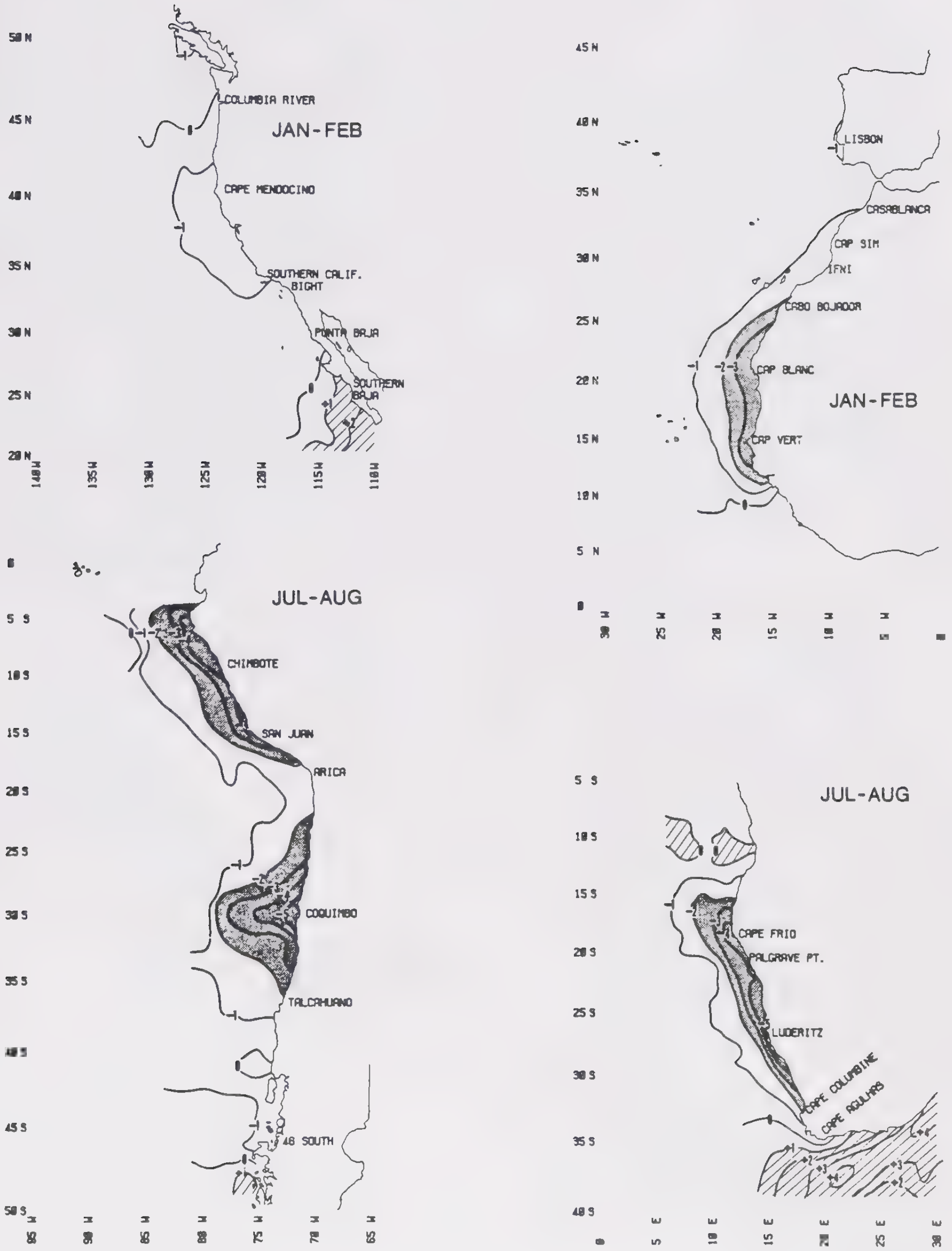

Chart 6. Winter coastal sea surface temperature anomaly (^{O}C).

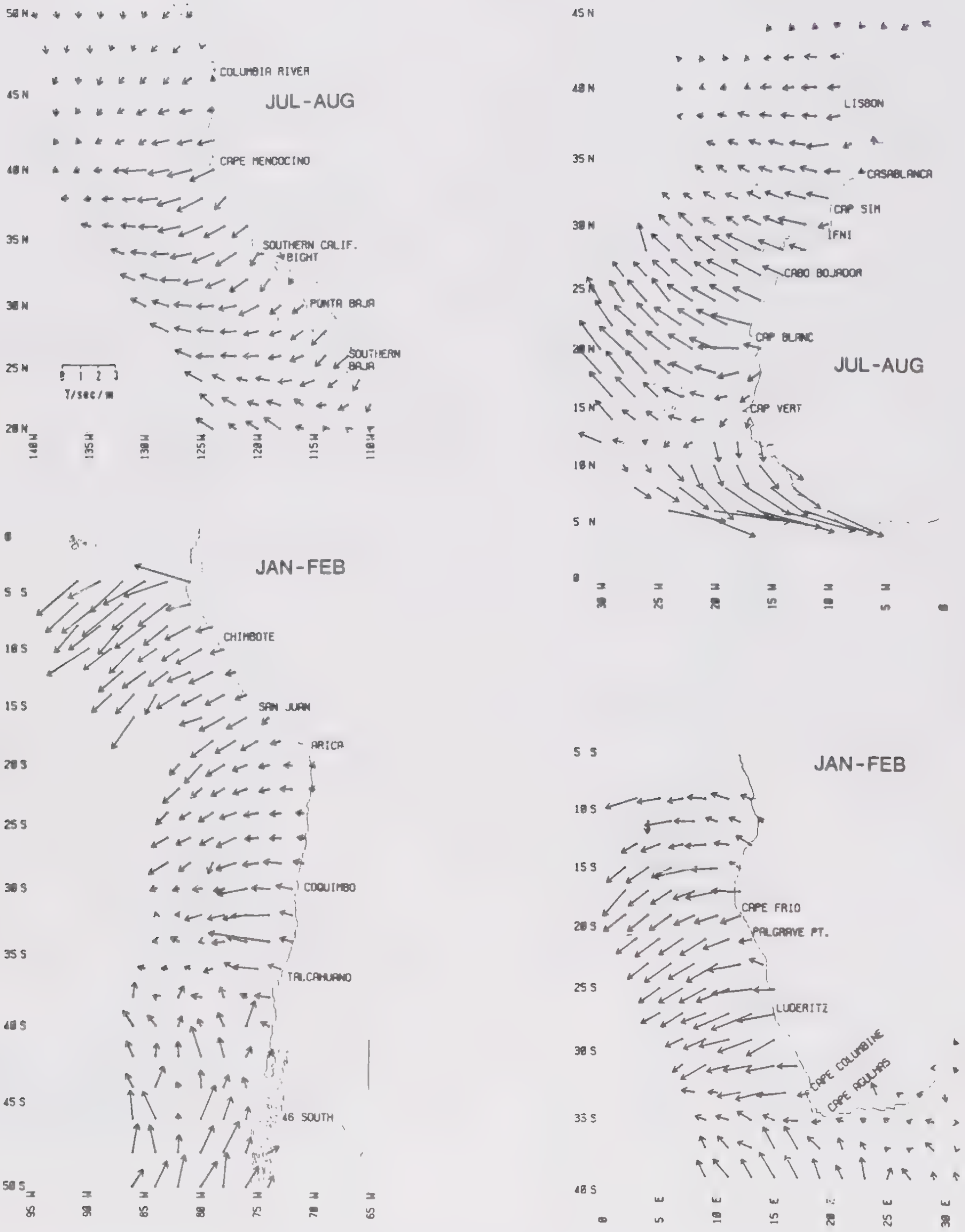

Chart 7. Summer surface Ekman transport (t $\sec^{-1}$ m^{-1})

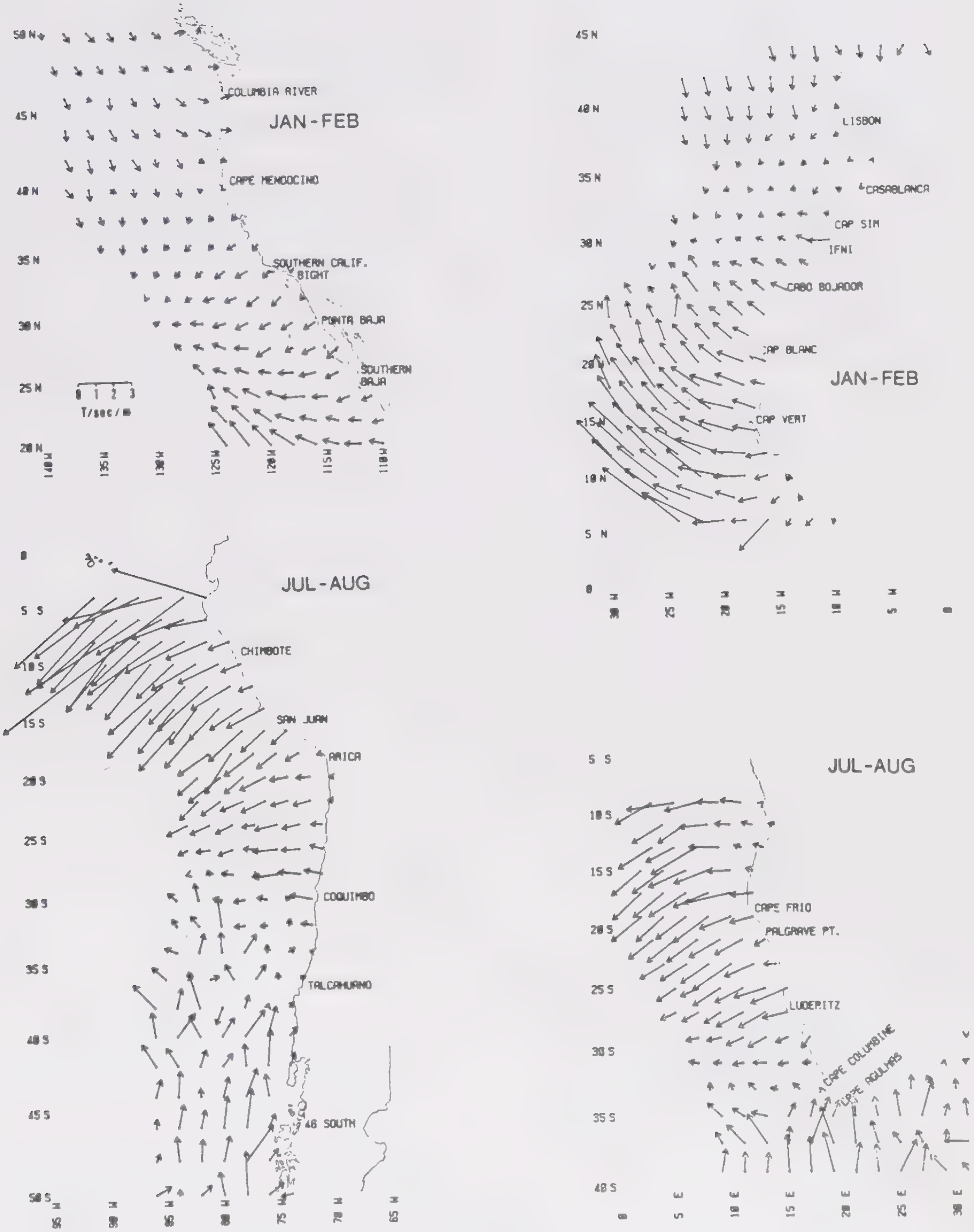

Chart 8. Winter surface Ekman transport (t sec^{-1} m^{-1})

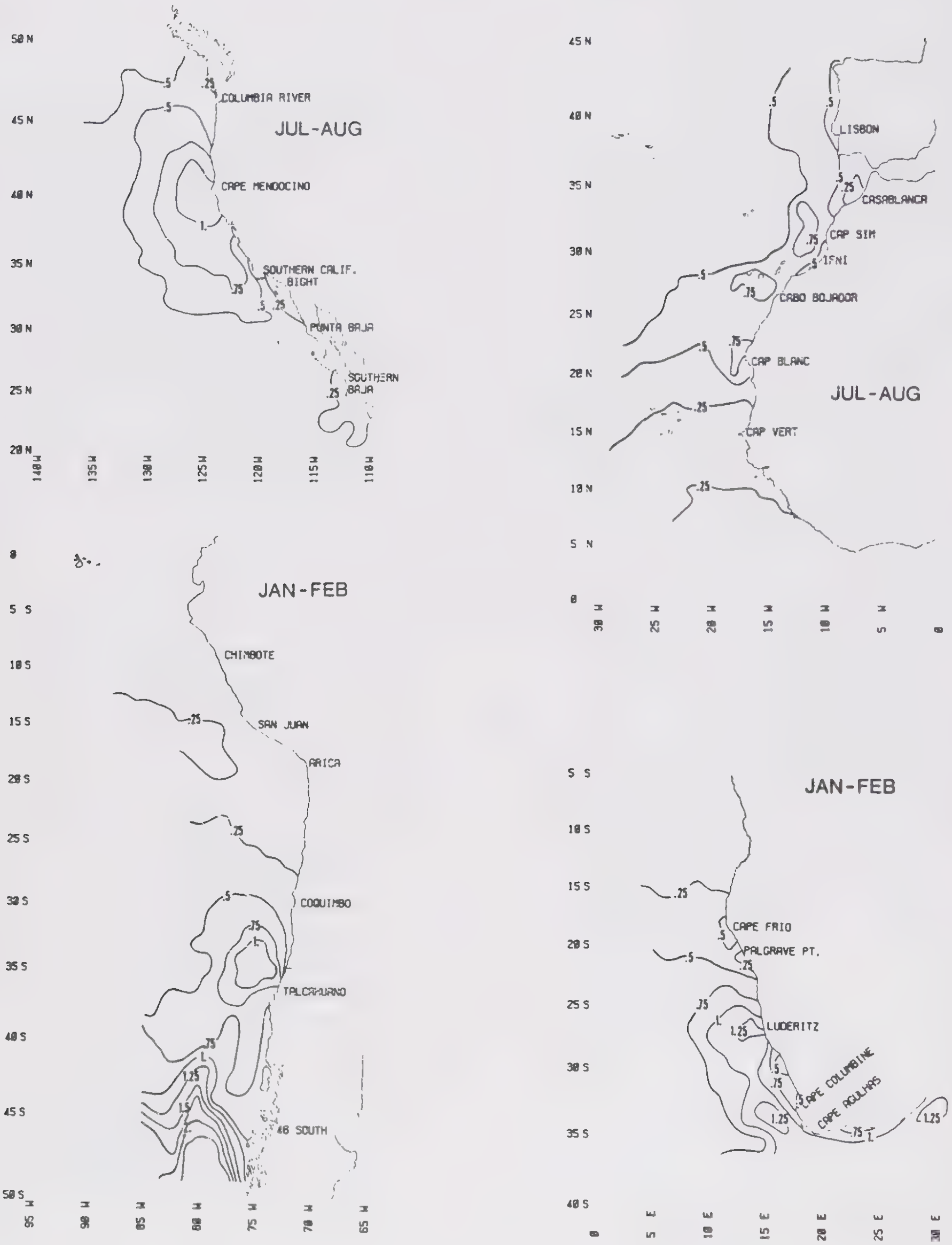

Chart 9. Summer distributions of wind speed cubed (units of 1000 m^3sec^{-3}).

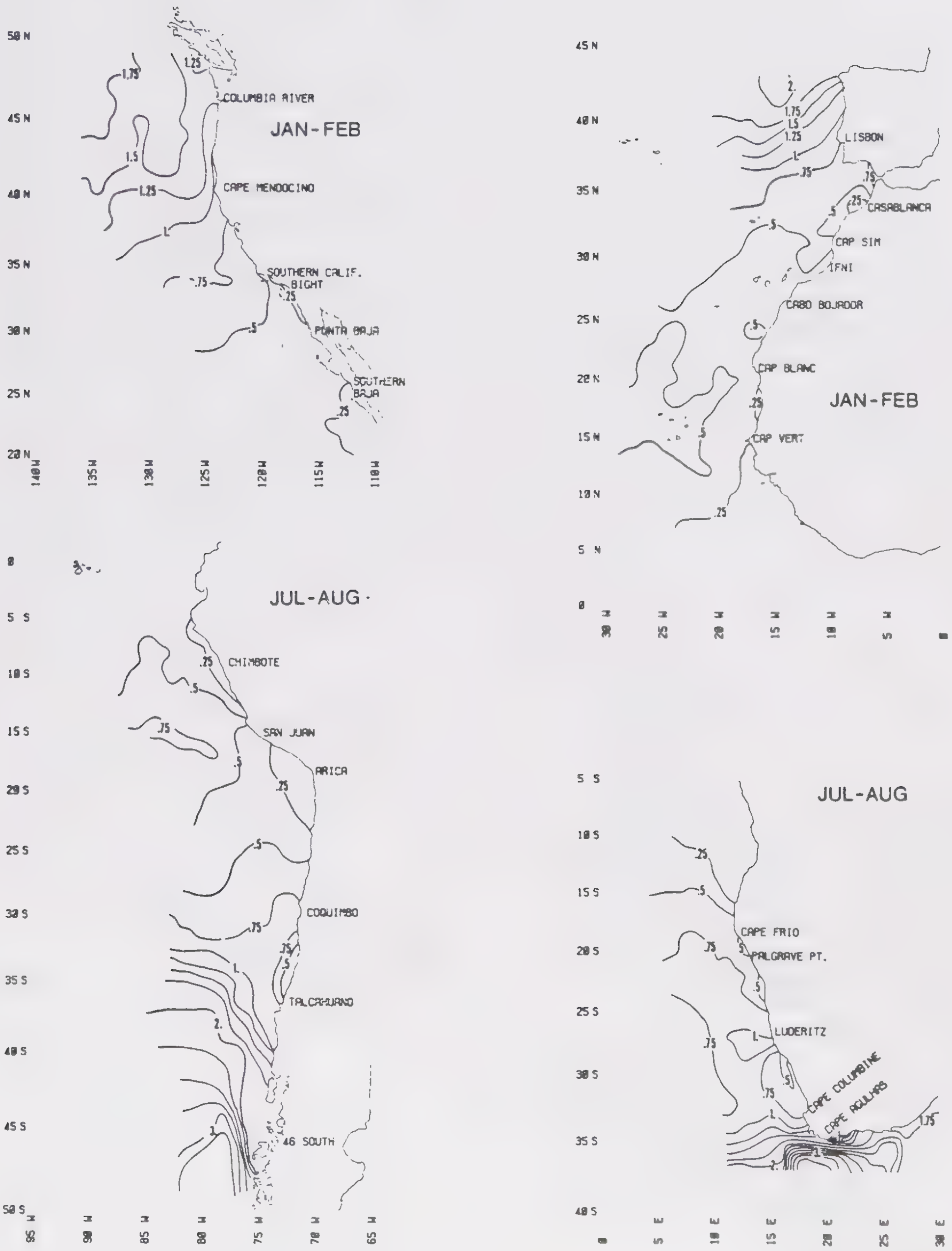

Chart 10. Winter distributions of wind speed cubed (units of 1000 $m^3 sec^{-3}$).

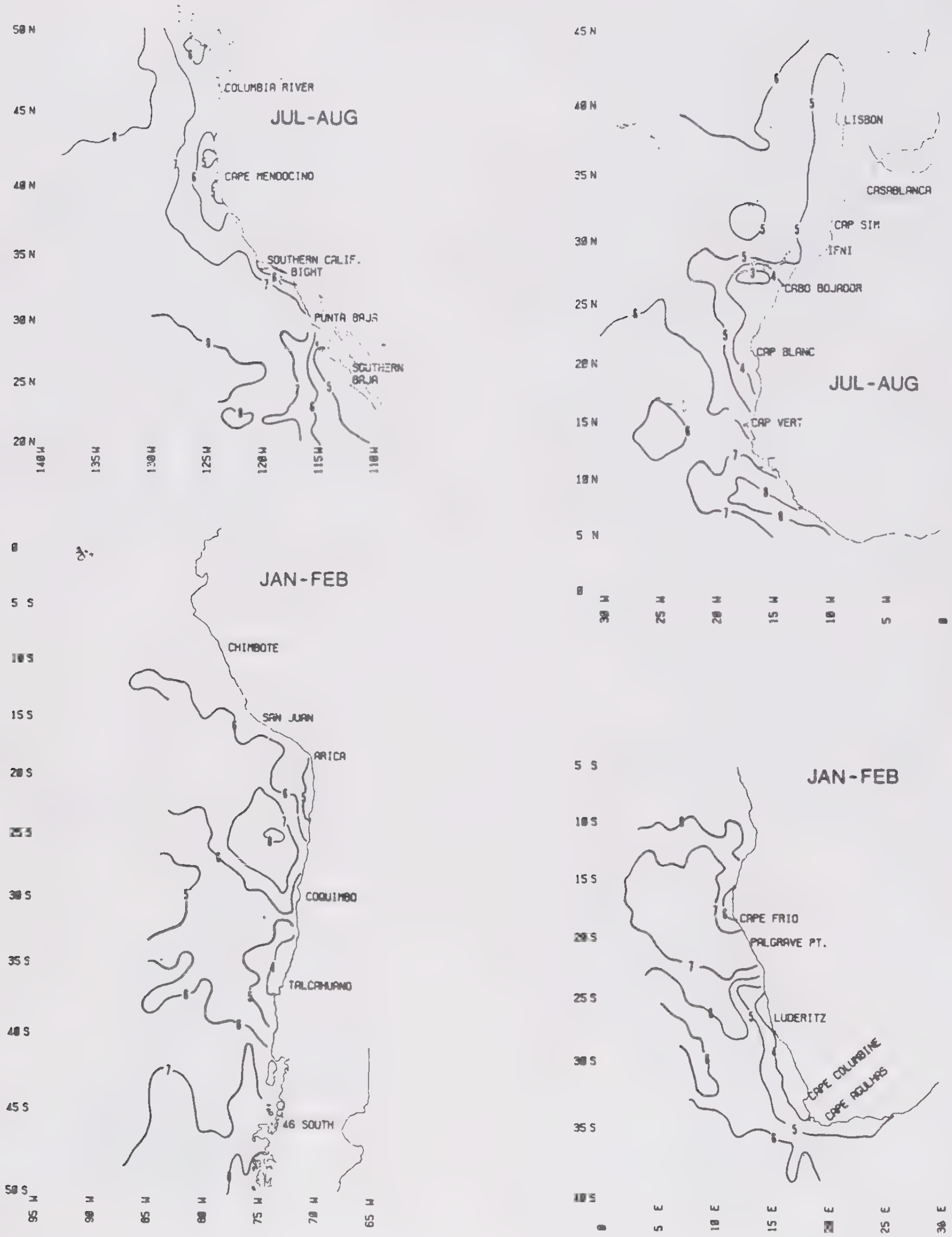

Chart 11. Summer distributions of total cloud amount (tenths of sky obscured).

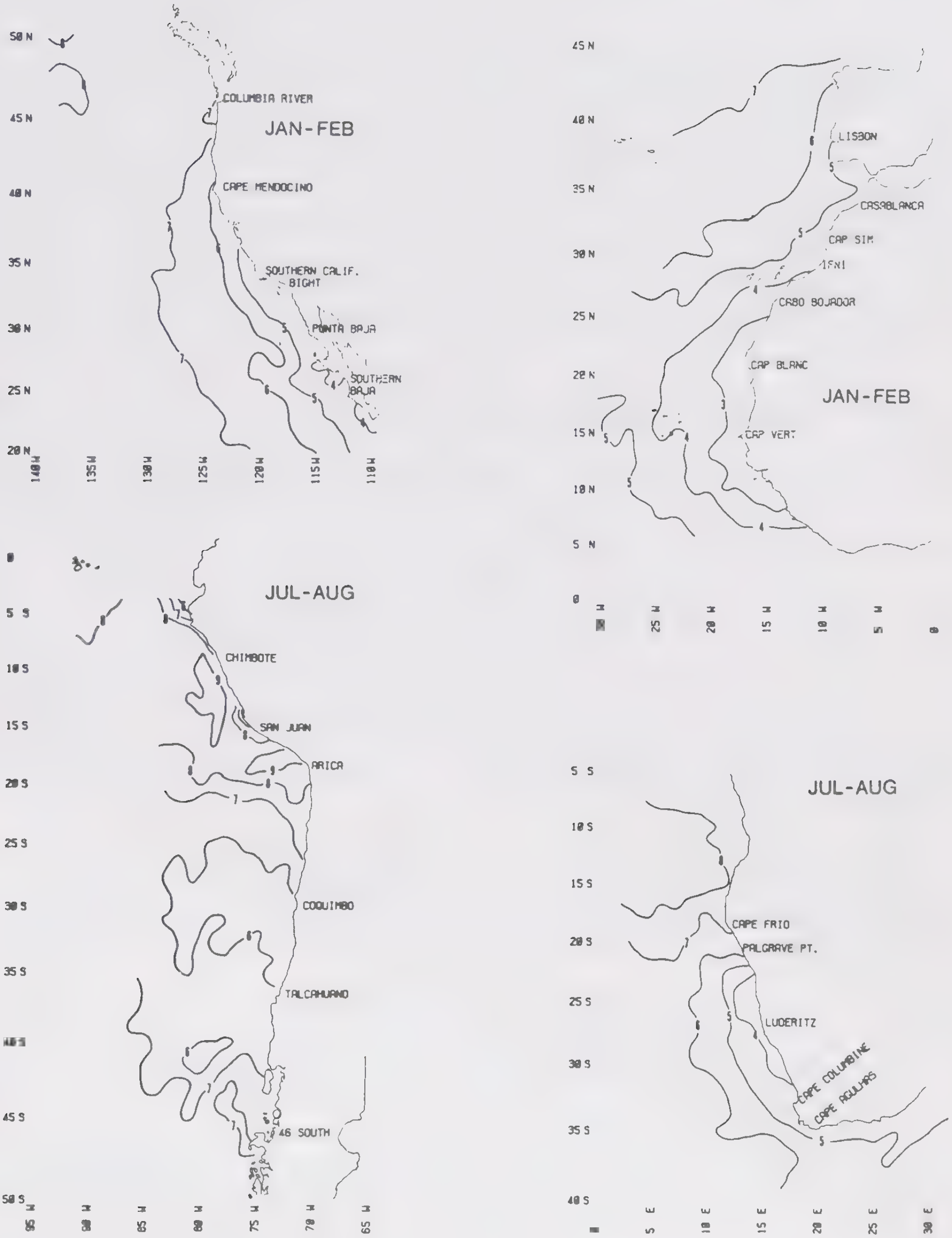

Chart 12. Winter distributions of total cloud amount (tenths of sky obscured).

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Annex H

Report of the Sub-Committee on Small Cetaceans

1. PARTICIPANTS, AGENDA AND INTRODUCTORY REMARKS

Members (M) of the Scientific Committee of the IWC, invited experts (E), observers (O) and interpreters (I) attending the meeting were:

Aguilar (M), Alverson (M), van Beek (M), Borodin (M), Braham (M), Brodie (M, O) Brown (M), Brownell (M), Caldwell (O), Cawthorn (M), Choi (M), Christensen (M), Collet (E), Dronenburg (M), Fortom-Gouin (M), Fraker (E), Gama (M), Glover (O), Gong (M), Gordon-Clark (O), Hammond (E), Holt (M), Ikeda (M), Jarrell (M), Kapel (M), Kasuya (E), Kato (M), Klinowska (M), Leatherwood (E), Misaki (I), Miyahara (M), Miyashita (M), Miyazaki (E), Nakamura (I), Ohsumi (M), Øritsland (M), Perrin (M), Pinta Gama (M), Riyazantsev (I), Rudge (M), Sanpera (M), Sigurjónsson (M), Skeat (M), Smith (E), Wada (M), Zemsky (M).

Many participants did not attend all sessions of the meeting.

Perrin chaired the meeting and edited the report. Alverson, Braham, Collet, Hammond, Kasuya, Klinowska, Leatherwood, Øritsland and Smith acted as rapporteurs.

The draft agenda was adopted with minor changes (Appendix 1). In the report, some rubrics have been modified from the agenda to accord with the course of the discussions.

2. DOCUMENTATION

Small-cetacean documents (SC/34/SM series) submitted to the Scientific Committee are listed in Apendix 2. Also containing information on small cetaceans and available to the sub-committee were SC/34/ProgReps Australia, Brazil, Canada, Denmark (Greenland), France, Iceland, Japan, Korea, New Zealand, Norway, South Africa, Spain, UK, USA and USSR; SC/34/Reps 1 (with Annex) and 3; SC/34/O 1, 3, 5, 13, 14, 21, 24, 25; SC/34/Sp9 and issues LXXXVII and LXXXVIII (bound together) of the International Whaling Statistics.

3. REVIEW OF STOCK ASSESSMENTS FOR SOME EXPLOITED POPULATIONS OF PELAGIC DOLPHINS (*DELPHINUS* AND *STENELLA* SPP.)

The sub-committee in 1981 agreed to focus this year on review of stock assessments for major exploited populations of pelagic dolphins. During the meeting, it was agreed to consider *Phocoena phocoena* and *Tursiops truncatus* as well as *Delphinus delphis* in the Black Sea fisheries.

3.1 Small-cetacean fishery in the Black Sea

3.1.1 Background

A fishery for three species, the common dolphin *Delphinus delphis*, the harbour porpoise *Phocoena phocoena*, and the bottlenose dolphin *Tursiops truncatus*, has existed in the Black Sea and the Azov Sea since 1870, as described in FAO (1978), Zemsky and Yablokov (1974) and Smith (1982). Four countries have been involved (Turkey, Rumania, Bulgaria and the USSR), with all but Turkey halting the fishery in 1966 following a collapse of the populations. The collapse was reportedly indicated by changes in the age, sex, species composition and size of the catch in 1964–65 (Zemsky and Yablokov, 1974).

The fishery by Turkey is not well documented. Danilevskiy and Tyutyunnikov (1968) in a discussion of the failure of the catch rates to increase to 1930s levels following the Second World War, note the existence of 'unceasing hunting of the dolphin with weapons in Turkish waters during the war and post-war years which destroyed the breeding stock and the young during the breeding season'. The same authors report 1951–56 catches of 85,000 to 100,000 centners (presumed hundreds of kilograms) by Turkey. The catches have been reportedly made from small boats using either high powered rifles or high calibre shotguns with large shot. Zemsky and Yablokov (1974) note that the loss rate of shot animals is very high. Zemsky reported that it may exceed 40 to 50%. A large number of dead harbour porpoise have been reported floating in parts of the Black Sea (see below).

3.1.2 Catch data

The recent data on the catches have been reported in several documents (Table 1). These data differ substantially among sources; some variability may be due to part-year or regional values being used.

The USSR catch prior to 1964 was 80 to 90% *D. delphis; P. phocoena* came to dominate in 1964 to 1966 (Danilevskiy and Tyutyunnikov, 1968). It is unclear if these percentages refer to numbers or weight of animals. The species composition of the Turkish catch is reported in Thornton (1982) as 80% harbour porpoise, 15–16% common dolphins, and 2–3% bottlenose dolphins. Common dolphins were still the preferred catch.

Zemsky and Yablokov (1974) estimated numbers of dolphins killed in the Turkish fishery by assuming an average weight of dolphins in the catch of 54 kg, but do not give the source of this value. Berkes (1977) uses a value of 50 kg. The mean weights of adult *D. delphis, P. phocoena* and *T. truncatus* are reported as 43 to 60 kg, 30 kg and 175 kg, respectively (Tomilin, 1957).

Thornton's percentages do not total 100; using the midpoint of the intervals given, and rescaling to 100%

yields species composition of 82, 16 and 2%. The percentages are assumed to refer to individuals and not to weight. Thus the average weight of the cetaceans would be

$$0.82 \times 30 + 0.16 \times 52 + 0.02 \times 175 = 36 \text{ kg}.$$

3.1.3 Population size data

Aerial surveys of dolphins have been conducted by the USSR since 1967. The numbers of schools of dolphins sighted by species and school size have been reported variously and have been used to estimate total dolphin population sizes by Zemsky and Yablokov (1974). They note that there are many uncertainties, and that the *D. delphis* estimates are more reliable than those for the other species because assumptions about spatial distribution were more likely met.

These estimates are also given by Smith (in press), where several of the assumptions made by Zemsky and Yablokov (1974) are examined. The estimates of the population size of *D. delphis* varied between 28,000 and 285,000 from 1967 to 1973, with no obvious trend. Similarly, the estimates of the population size of *P. phocoena* varied between 12,000 and 33,000 over the same period. Several of the assumptions in these estimates are not tested, and the effect of sea state on strip transect methods has not been accounted for.

Table 1

Reported catches of dolphins by Turkey, in units as originally reported, for all years where data are available since 1965. Values are given by source because considerable uncertainty exists about these data and they have been quoted variously in different units, using various conversion factors

Year	Danilevskiy and Tyutyunnikov (1968)[1]	Zemsky and Yablokov (1974)[2]	Berkes (1977)[3]	FAO (1979)[4]	Thornton (1982)[5]
1964	—	—	—	—	429
1965	—	—	1.300	—	—
1966	2,000	—	5,900	—	—
1967	540	2.100	200	—	5.900
1968	—	20,200	2,200	—	2,200
1969	—	—	8,300	—	8.346
1970	—	—	3,400	4,900	7,055
1971	—	—	4,400	4,400	—
1972	—	19,000	4,400	3,200	4.400
1973	—	70,000	4,400	2,600	2,200
1974	—	—	—	2,250	—
1975	—	—	—	2,080	1,404
1976	—	—	—	1,907	1,590.3
1977	—	—	—	1,907	2,608.3
1978	—	—	—	1,907	1,907.8
1979	—	—	—	1,907	1,827.9
1980	—	—	—	—	2,721
1981	—	—	—	—	325

[1] In centners; 1966 and 1967 values are approximate amount sold to the fat/meal factories in Trabzon; 1967 value is for first half of year Data reported to be from monthly surveys of fisheries in Turkish magazine *Balik ve Balikcilik*.

[2] In centners; 1967 value reported to be from *Balik ve Balikcilik*, 1966, but may have been taken incorrectly from Danilevskiy and Tuytyunnikov (1968); 1968 and 1972 values from *Balık ve Balikcilik* in 1969 and 1973, respectively.

[3] In tonnes; 1972 and 1973 values estimated, basis unknown.

[4] In tonnes; 1977 to 1979 values estimated, basis unknown

[5] In tonnes; source given as: 1964, 1967–71, 1972–74, 1975 values from Berkes (1977), and Turkısh State Institute of Statistics. Su Urunleri Anket Sunuclari, 1971 and 1974; 1975–81 values from Turkish State Institute of Statistics, Su Urunleri Anket Sunuclari. Fisheries Statistics, 1972–75, 1976–79, 1980, and personal communication with H. H. Hatipuglu, Manager, + ve Balik Kurumu, Trabzon, the processing station for fish and dolphins.

More recent aerial sighting data were available to the sub-committee showing the numbers of schools sighted in the USSR from 1978 to 1980, by species and school size (Table 2). The number of schools sighted varied widely among years; the percentage of schools of each species varied less. Mean school sizes were relatively constant, with overall means of 10.4, 9.5, and 13.2 for *D. delphis*, *T. truncatus* and *P. phocoena*, respectively.

Table 2

Number of dolphin schools sighted during approximately 8,000 km tracks of aerial sighting surveys by the USSR in the Black Sea area during 1978, 1979 and 1980, for each species classified by estimated school size. The surveys reportedly followed the same tracks in each year.

	Estimated school size (midpoint of intervals)										
Species	5	15	25	50	75	100	150	200	300	500	Total
1978											
D. delphis	82	21	5								108
T. truncatus	22	17	1	2		1					43
P. phocoena	5	3	1								9
1979											
D. delphis	380	83	22	7		3		1		1	497
T. truncatus	103	31	1	1		1					137
P. phocoena	19	3									22
1980											
D. delphis	112	41	12	2	1	1		2			177
T truncatus	57	22	1	3	1						84
P. phocoena	8	8									16

Maps of the location of sighted schools showed *D. delphis* and *T. truncatus* distributed widely in all areas surveyed, but variably among years, and *P. phocoena* distributed exclusively in the eastern half of the sea, primarily but not exclusively nearer shore.

Smith reported that additional dolphin sighting data were collected during a joint USSR–US research cruise in the southeastern Black Sea in June 1981. Although limited to four days and approximately 900 km of trackline, the survey results provide some information on sighting rates and school sizes by species, and on ranges in the area 39 to 41°E longtitude and 41 to 43°N latitude. Only three *T. truncatus* schools were seen, all near the coast. Twenty four schools of *D. delphis* and 35 schools of *P. phocoena* were seen in both coastal and open waters, with average school sizes of 36.3 and 4.4, respectively. Thus the rates of encounter of individual dolphins were 0.99 and 0.17 per km searched, for *D. delphis* and *P. phocoena*, respectively. Also during this survey, 17 dead *P. phocoena* were sighted, floating. They were encountered at decreasing rates per km of 0.036, 0.017, 0.011, and 0.010 on successive days as the ship surveyed increasingly more northerly east-west tracks, moving farther away from Turkey.

3.1.4 Reproductive rate data

Few data are available on reproductive rates for dolphins in the Black Sea, and none are available from recent years. The proportion of all *D. delphis* females in the catches in 1931–32 which were pregnant and which were lactating are shown in Table 3, along with comparable figures from eastern tropical Pacific populations. The percentage pregnant for the more exploited Black Sea populations

Table 3

Reproductive indices for *Delphinus delphis* in the Black Sea and in the eastern tropical Pacific

Population	Year(s)	N	% of all females pregnant[1]	% of all females lactating[2]
Black Sea				
(a) Danilevskiy and Tyutyunnikov (1968)	1931	158	22.0± 6.6* (15.4–28.6)	13.0± 5.4 (7.6 – 18.4)
(b) Klumov (1954)	1931	932	11.9± 2.1 (9.8–14.0)	21.1± 2.7 (18.4 – 23.8)
	1934	3,320	11.5± 1.1 (10.4–12.6)	29.9± 1.6 (28.3–31.5)
	1939	680	12.2± 2.5** (9.7–14.7)	15.9± 2.8 (13.1–18.7)
Eastern tropical Pacific (Henderson *et al.*, 1980; Perrin and Oliver 1982; SC/34/SM5)				
Northern	1973–81	124	28.3± 8.1 (20.2–36.4)	39.1± 8.8 (30.3–47.9)
Central	1973–81	722	17.2± 2.6 (14.4–20.0)	30.9± 3.4 (27.5–34.3)

[1] % pregnant: 3 of 4 lowest estimates are for Black Sea; highest estimate is for ETP little-exploited population.

[2] % lactating: great variation, but 2 of 3 high estimates are for ETP.

* Approx. 95% confidence interval = ± 2 S.E. estimated as $2\sqrt{p(1-p)/n}$.

** All with corpora lutea assumed pregnant.

(see SC/34/SM6 for status of the Pacific populations) might be expected to be higher, but no consistent differences are apparent. Percent lactating was lower in the Black Sea, as might be expected. No recent estimates of natural mortality rates and gross or net reproductive rates are available.

3.1.5 Population status

The catch data in Table 1 are unsatisfactory because numbers and species of dolphins killed are not indicated. Thus assessments by species are not feasible. Assuming average body weights of 36 kg, the reported catches, which range from 2,000 to 8,000 tonnes per year since 1967, suggest varying kill levels of 56,000 to 222,000 animals of the three combined species, per year. The total number of cetaceans harvested from 1967 to 1981, making the same assumptions, was approximately 1,300,000 animals.

The population size estimates and sighting data are unsatisfactory because many untested assumptions must be made to obtain the total abundance estimates. Additionally, the results of the aerial sighting surveys are highly variable among years, suggesting that some factors affecting sighting rates have not been accounted for. The recent shipboard sighting survey data are too limited to allow population size estimates. If, however, one takes the average of the population size estimates given by Zemsky and Yablokov (1974) as reasonable, then the total number of animals of even all three species (264,000) would appear to be too small to have supported the above-discussed possible levels of harvest. Even the maximum population size estimates for the three species combined given by Zemsky and Yablokov (1974) was only 432,000, less than one third of the possible number of dolphins killed from 1967 to 1981.

Zemsky offered the opinion that although his population size estimates are quite uncertain, the Black Sea is neither large enough nor productive enough to have ever supported more than 600–700,000 animals, even in the absence of a fishery. This opinion, coupled with the fact that the Soviet fishery was stopped due to decline of catches, suggests that either the Turkish fishery is having a very serious impact on the population, or there are some substantial errors in some of the data.

The dead *P. phocoena*, at apparently decreasing densities based on the declining sighting rates with distance from the Turkish coast, suggest that the fishery may be rather wasteful, as is generally known to occur in rifle fisheries.

The Turkish catches for 1981 were reported to be much lower than in recent years, due to restrictions on the export market to the European Economic Community. The Turkish markets for dolphin products are not known, and the long-term impacts of the EEC restrictions are not predictable.

Turkey has not yet ratified the Council of Europe (Berne) Convention; ratification may be done with exeption. If Turkey comes under the complete provisions of this Convention, then these animals will become protected species in Turkey from June 1982.

The catches of anchovy are reported to be increasing rapidly in the eastern Black Sea; because the cetaceans in this area are thought to feed on anchovy, the sub-committee noted with concern the reported recent increases in the Black Sea anchovy fisheries by both Turkey and the USSR. There is insufficient information available to assess the likely impacts of the anchovy catches on the cetacean populations.

3.1.6 Recommendations

The sub-committee prepared a set of recommendations for improvement of harvest statistics, analysis of existing aerial survey data, invitation to the Scientific Committee meeting of individuals in Turkey knowledgeable of the fishery, study of dolphin/anchovy fishery relationships, and sampling of the catch for data on sex, length and age composition and reproductive condition (see Agenda Item 10 of this report).

3.2 *Stenella* spp. in the eastern tropical Pacific

3.2.1 Background

In the eastern tropical Pacific, dolphins of several species and stocks are killed incidentally in the purse-seine fishery for tunas. Fishermen take advantage of the occurrence of mixed-species aggregations of tuna, dolphins and birds in this region, using it to locate and capture tuna. The purse-seine net is set around schools of dolphins and the tuna swimming beneath them, and although effort is made to ensure the release of the dolphins unharmed, some are killed during the fishing operation. The fishing vessels of thirteen nations (1981 figure) use this method of catching tuna in the eastern tropical Pacific (SC/34/SM2) in a large area comprised of international waters and the coastal waters of Central and South American nations (SC/34/SM1).

The major stocks of dolphins that have been involved incidentally in this fishery are the northern offshore stock of the spotted dolphin (*Stenella attenuata*) and the eastern and northern whitebelly stocks of the spinner dolphin (*S. longirostris*). Approximate ranges of these stocks are given in SC/34/SM1. Major exploitation is thought to have begun in 1959 following technological changes in purse-seine fishing gear. Available data suggest that incidental

Table 4

Estimated number of dolphins (thousands) killed incidental to the tuna purse seine fishery in the eastern tropical Pacific, from 1959 to 1981. Estimates are given by population of dolphins of the genera *Stenella* and *Delphinus*, and of other unidentified species combined for the fleets of all nations. Data for all species for 1979–81 from SC/34/SM2, Table 4. Estimates from 1959 to 1972 are based on the mean numbers of dolphins killed per set from 400 sets observed on 21 fishing trips from 1964 to 1972, pooled for all years. Estimates from 1973 to 1978 based on the mean number of dolphins killed per set for each year, assuming US and non-US mean kill rates were different. Estimates from 1979 to 1981 based on the mean number of dolphins killed per set, stratified by US and non-US vessels. Estimates of the non-US kill levels have large sampling errors and are different from estimates based on the ratio of numbers of dolphins killed and numbers of tons of tuna caught

Year	*S. attenuata*[1] offshore spotted	*Stenella longirostris*[1] Eastern spinner	Whitebelly spinner	*S. coeruleoalba*[2] striped	*D. delphis*[2] common	Other[2] and unidentified	Total
1959	68	26	0	0	4	0	98
1960	341	127	0	0	20	0	488
1961	384	143	0	0	22	0	549
1962	159	59	0	0	9	0	227
1963	175	66	0	0	10	0	251
1964	292	110	0	0	16	0	418
1965	322	120	0	0	18	0	460
1966	292	110	0	0	33	0	435
1967	197	73	0	0	11	0	281
1968	170	64	0	0	9	0	243
1969	348	116	14	0	19	0	497
1970	339	113	13	0	18	0	483
1971	168	56	7	0	9	0	240
1972	275	92	11	0	15	0	393
1973	125	31	31	0	28	0	164
1974	91	25	45	0	5	0	166
1975	100	43	32	1	3	0	149
1976	45	9	19	3	7	1	80
1977	21	5	5	0	18	0	49
1978	18	2	4	1	3	0	28
1979	12	1	2	1	7	1	23
1980	22	2	11	1	7	0	43
1981	33	2	7	0	1	3	47

[1] Data for *Stenella attenuata* and *S. longirostris* for 1959–78 from SC/34/SM6, Table 4—numbers divided by 1.048 to remove injured animals.

[2] Data for other species for 1959–78 from Smith (1979) Table 15—numbers divided by 1.017 to remove injured animals.

mortality increased rapidly from the early 1960s to levels estimated at several hundred thousand animals per year during the mid-1960s and early 1970s (Table 4). Mortality declined rapidly through the 1970s, and present levels are estimated to be of the order of tens of thousands per year. Although the offshore spotted and eastern spinner have been exploited since 1959, the whitebelly spinner was not exploited until approximately 1969, following an offshore expansion of the tuna fishery (Table 4).

The non-US registered vessels are thought to have been responsible for a small proportion, increasing over time, of the dolphins killed from 1959 to 1972. From 1973 to 1978 the proportion of the estimated dolphins killed which are thought to be due to non-US vessels varied from 0.15 to 0.51, and again increasing generally over time. Estimates of the proportion of the kill due to non-US vessels from 1979 to 1981 are given in Table 5, varying from 0.20 to 0.62 over years and for two different methods of estimating the total kill. The sample variances of the total kill estimates for the non-US fleet are large, but it is clear that the proportion of the kill due to the non-US fleet is increasing.

Research on levels of mortality, abundance and biological parameters of these dolphins has been pioneered by the United States. Some preliminary work was done in the 1960s, but in the early 1970s the US began to place observers on purse-seiners of the US fleet to collect data and life-history samples. A similar programme was initiated by the Inter-American Tropical Tuna Commission (IATTC) in 1979 to sample fishing vessels of the international fleet. Both these programmes are continuing. In addition, since the early 1970s the US has had an extensive research programme utilising research vessels and aircraft to collect data for stock assessment.

3.2.2 *Most recent stock assessments*

In 1976, the US convened a workshop in La Jolla, California to assess the status of the stocks of these exploited dolphin populations. The major result of this assessment was that the eastern spinner was declared a protected stock by the US, so that vessels of the US fleet were forbidden to set their nets around schools containing eastern spinners.

Table 5

Estimated number of dolphins (thousands) killed incidental to the tuna purse seine fishery in the eastern tropical Pacific, from 1979 to 1981, for vessels registered in the United States (US) and not registered in the US (non-US). Estimates are given for all species (with standard deviations in parentheses), based on the mean number of dolphins killed per set (KPS), and, alternatively, on the ratio of numbers of dolphins killed per ton and the tons of tuna caught per set (KPT)

	KPS		KPT	
Year	US	Non-US	US	Non-US
1979	16.4	6.5	16.4	4.0
	(1.6)	(2.2)	(1.6)	(2.1)
1980	17.0	26.3	18.6	31.0
	(1.7)	(6.7)	(1.6)	(6.8)
1981	17.9	28.7	18.5	16.5
	(1.5)	(20.5)	(1.9)	(9.8)

Note: Estimates of the non-US kills of dolphins have large sample variances due to very limited or lacking data from several countries, including Bermuda, British Grand Cayman Islands, Ecuador, Republic of Korea, Mexico, Netherlands Antilles, Portugal, El Salvador, Senegal, Spain and Venezuela. The proportion of the kill which is due to some of these countries is thought to be quite large, and lack of data will make obtaining precise estimates impossible.

In 1979, a similar workshop was convened which estimated current and initial levels of abundance of the exploited stocks and the most likely level of maximum net productivity for those populations. A summary of this assessment is given in SC/34/SM6, which describes a simple model to back-calculate initial abundance from estimates of current abundance using primarily research vessel and aircraft data, from estimates of annual mortality (using data collected from fishing vessels) and from estimates of net reproduction. The eastern spinner population was estimated to be at approximately 20% of its initial size, the northern offshore spotted to be at approximately 40–50% and the northern whitebelly spinner to be at approximately 70–80% of initial size. The sub-committee noted that Table 4 in SC/34/SM6 is not in the source document referenced.

Following this workshop, there were legally-required hearings in the US centring on the issuance of a permit to the tuna fleet allowing US vessels to set their nets around schools of dolphins. Some additional data and the results of some new analyses were presented during these hearings, which culminated in an Administrative Law Judge's decision, which in turn led to some administrative adjustment to the conclusions of the workshop. The eastern spinner remained a protected stock whilst the offshore spotted and the whitebelly spinner remained unprotected, with mortality quotas for the following five years.

Document SC/34/SM1 describes an analysis of sightings data collected by observers aboard tuna purse-seiners. Estimates of abundance have been presented for 1977–81 in order to investigate possible trends. Potential biases in the estimates and the size of their standard deviations dictate that little information can be obtained from the results. However, there were definite decreasing trends in estimates of mean school size for offshore spotted and the eastern and whitebelly spinner dolphins.

Discussion of the current status of the stocks of these dolphins centred on the problems in estimation of current abundance levels and how the proportion of current to initial population size might change with different levels of current abundance. Members of the sub-committee expressed concern over several aspects of this estimation procedure, mostly involving suitable ways of stratifying the data; for example, by area and by searching effort under different sighting conditions. Correction factors were mentioned for these and other factors of the analyses such as estimated mean school size, which is different when calculated using data collected in fishing vessels, research vessels and aircraft.

The sub-committee decided to calculate proportions of current to initial abundance for the estimated 95% confidence limits of the current population estimates given in SC/34/SM6 in order to investigate the range of proportions likely when using interval estimates of current abundance. This was done by assuming net reproduction to have been zero, thus allowing initial population size to be calculated by simple addition of the total estimated number of animals killed during the period of exploitation to the current population size. It was recognised that the inclusion of net reproduction would alter the results in a manner which could be assessed from SC/34/SM6. Table 6 shows these proportions together with those from SC/34/SM6 for the point estimates of current population size.

The sub-committee recognised that there was little that could be said concerning the status of these stocks based on the variation in the estimates of proportions of current to initial population size (Table 5). Members noted that the US is planning a major assessment in 1984 and voiced their support for this action. By then, a considerable amount of new information should be available, and some of the uncertainties and variation in the estimation procedures should be reduced.

3.2.3 *Other relevant information*

The sub-committee noted that several documents (SC/34/SM2,5,6) contained information relating to estimates of mortality and one (SC/34/SM3) contained information on efforts being made to reduce mortality by means of improvements and new technology in fishing methods.

Members were concerned, as in the sub-committee meetings of the last two years, that estimates of mortality for the non-US fishing fleet (comprising vessels from some dozen nations) were far more imprecise than estimates for the US fleet (SC/34/SM2). Furthermore the very small sample of non-US vessels and its lack of representation of the non-US fleet dictated that it could not be determined whether or not US and non-US rates were different. The sub-committee noted that several member nations of the IWC (Mexico, the Netherlands, Spain and the UK) had vessels that fished for tuna associated with dolphins in 1981 but did not participate in the observer programme of the IATTC which collects the mortality data for the non-US fleet. However, it was pointed out that the UK is participating in 1982. At last year's meeting, the sub-committee was informed that Mexico was initiating a programme of data collection and that this would be reported on this year. Unfortunately, no report has been received by the sub-committee. In view of the fact that the non-US tuna fleet in the eastern tropical Pacific is increasing in size (especially the Mexican fleet; Anon, 1982) relative to the dominant US fleet, the sub-committee

Table 6

Proportions of current to initial population size of *Stenella* spp. assuming zero net reproduction based on 95% confidence limits of the current population sizes estimated in SC/34/SM6, using research data only (R) and fishing vessel plus research data (F + R)

	Estimated 95% confidence limits of the estimates of current population, in thousands		Estimates of proportions of current to initial population size	
	F + R	R	F + R	R
Offshore spotted	1,250–4,300	740–2,630	0.23 (0.40) 0.51	0.15 (0.29) 0.39
Eastern spinner	164–422	151–435	0.10 (0.17) 0.23	0.10 (0.17) 0.23
Whitebelly spinner	110–650	81–350	0.37 (0.66) 0.77	0.30 (0.53) 0.65

Note: figs in parentheses represent the mean values felt that members of the IWC whose vessels fish for tuna associated with dolphins should be strongly encouraged to participate in the IATTC programme of data collection.

3.2.4 Conclusions and recommendations

The sub-committee concluded that further analyses are necessary before any reliable statements can be made about the status of the offshore spotted and eastern and whitebelly spinner stocks in the eastern tropical Pacific. Several recommendations are suggested concerning participation in the IATTC programme, mortality reduction, re-assessment of the stocks, and reporting of statistics (see Agenda Item 10.2).

3.3 *Stenella coeruleoalba* in the western North Pacific

3.3.1 Background

A large catch by Japan in 1980 (approximately 16,000, *Rep. int. Whal. Commn* 32: 179–83) considered in relation to estimated MSY of 5–6,000 led the sub-committee to place this item on its agenda for 1982. The sub-committee notes that in 1981 the fishermen voluntarily held the catch to 4,710 under advice offered by the Japanese Fisheries Agency (SC/34/SM10).

The sub-committee had available to it two relevant documents: SC/34/SM10 on the history, catches and the nature of the fishery, and SC/34/SM12 on historical changes in reproductive parameters.

The fishery is known to have existed since at least 1888 (the Meiji period), but dolphins of unidentified species were taken in drive fisheries at least as long ago as in the Genroku Ages (1688–1703). At present, about 97% of the catch is taken at Kawana and Futo on the Izu Peninsula and Taiji on the Kii Peninsula in southeastern Honshu. Annual total catches have fluctuated greatly from near zero levels in some years to more than 20,000 in others.

3.3.2 Status of the stock

The most recent stock assessment was carried out in 1975 by Kasuya and Miyazaki (1982), based almost entirely on history of catch and analysis of life-history specimens and data collected in the fishery. They estimated MSY level on the basis of a deduced relationship between stock size and recruitment, incorporating consideration of age-specific vital rates and inferred density-dependent changes in rates. They estimated initial population size at 320,000–340,000 and MSY level at 161,000–170,000. MSY was estimated at 4–6,000, near the RY in 1974. Kasuya reported at this meeting, however, that more recent life-history and population studies led him to believe that these estimates are unreliable, for reasons discussed below.

The record of catches is not complete, but complete statistics from 1962 onwards (Fig. 2 in SC/34/SM10) indicate a statistically significant downward trend in total catches on the Izu Peninsula over the period 1962 to present. The full statistics for earlier years are not available, but some annual catches are known to have exceeded 20,000 dolphins, a level not reached during the 1962 to 1981 period. Factors contributing to the very wide fluctuation in catches are known to include market demand, starting and stopping of fisheries at various villages, competition or cooperation between villages, changes in numbers of teams per village, changes in speed of scouting vessels, long- and short-term oceanographic variation, fluctuations in mean school size and in timing of seasons and, most recently, advice by the Japanese Government that catches be reduced. Large volumes of data are reported in SC/34/SM10 and in numerous other reports, published mainly in *Sci. Rep. Whales Res. Inst., Tokyo*, but the above listed factors are confounded, making adequate analysis of the presented data difficult if not impossible. Two serious problems with the effort data are that while periods of scouting last only hours, effort is reported in days, and CPUE on one day influences effort on the following and successive days. Clearly, the effects of the many factors must be isolated before CPUE can be evaluated with any confidence.

SC/34/SM12 reported findings that indicate that some reproductive parameters changed over the period of the 1950s to the 1970s: average age at attainment of sexual maturity in females (from 9.7 years in the 1956 cohort to 7.2 years in the 1970 cohort), minimum age at attainment of sexual maturity (in parallel with average age), and average length of reproductive cycle (from 4.0 years in 1955 to 2.8 years in 1977, mainly through shortening of the lactation period). Kasuya cautioned, however, that these last findings may not be completely reliable for two reasons: (1) age and sex segregation is pronounced in the population, yielding several types of schools, but only 37 'schools' were sampled over the period of the study, 1967–80, and half of them were small schools; and (2) schools examined before 1967 were sampled by different workers than were the later, majority of schools. The results are important, however, in that they are consistent with a hypothesis of increased reproductive rate as a density-dependent response to exploitation.

3.3.3 Conclusions and recommendations

The sub-committee was able to agree that:

1. Total catches have declined over a long period on the Izu Peninsula.
2. There is no clear trend in CPUE as reported.
3. Some reproductive parameters have probably changed in a way consistent with density-dependent response.
4. It is very difficult to assess a migratory population at one point along its migration route, as is the case here.
5. There are considerable uncertainties and problems involved in analysis of the CPUE and more detailed data and renanalyses are needed.

The sub-committee drafted a recommendation to address the problems of the CPUE analyses (see Agenda Item 10.3).

4. REVIEW OF BOTTLENOSE WHALE POPULATIONS AND FISHERIES

4.1 Northern bottlenose whale, *Hyperoodon ampullatus*

Sightings were reported in SC/34/O 5 and O 6. There were no takes of this whale in 1981. The status of this stock remains unknown, and its continued protection is recommended (see Item 10.4).

4.2 Southern bottlenose whale, *Hyperoodon planifrons*

There was no new information available on this species.

4.3 Baird's beaked whale, *Berardius bairdii*

(also referred to as 'northern giant bottlenose whale').

The sub-committee reviewed and discussed the two submitted documents on Baird's beaked whale in the western North Pacific (SC/34/SM8 and 11).

4.3.1 Distribution, stock identity and migrations

Sightings by Japanese scouting boats from 1965 to 1980 show that the Baird's beaked whale is widely distributed across mid-latitudinal waters of the North Pacific from about 30°N northwards into the southern Bering Sea (SC/34/SM11).

Recorded southern sightings down to about 25°N in the Western and Central Pacific and south of 40°N in the Eastern Pacific (SC/34/SM11) are subject to some doubt because surveys by other investigators, as reported by Leatherwood, indicate that very few Baird's beaked whales occur at water temperatures above 18°C in the Eastern Pacific, north of those lower latitudes where they were reported by the Japanese scouting boats. However, Kasuya reported that Baird's beaked whales have been hunted from Chiba during the presence of the warm Kuroshio current. Misidentification of *Berardius* cannot be excluded as an explanation of the southern distribution of scouting boat sightings, particularly in the warm waters near Hawaii. Leatherwood reported the occurrence of an unidentified or undescribed species of large beaked whale in the central tropical Pacific (Leatherwood *et al.*, 1982). Kasuya noted that other beaked whales, e.g. *Ziphius*, may be included in the scouting boat data. This potential problem merits further investigation.

The absence of sightings in areas off the east coast of Japan (Fig. 4, in SC/34/SM11) suggests a discontinuity in distribution and hence a discrete stock in Japanese waters. However, low sighting effort in these areas may account for the apparent separation. Marking studies have not been conducted, and no other information is available that would indicate stock structure. A pan-Pacific stock of Baird's beaked whales cannot therefore be ruled out with the present state of knowledge. Analysis of sightings relative to sighting effort by area (smaller strata, if possible) might throw some light on this problem.

Although catches are taken in discrete local areas (Omura *et.al.*, 1955; SC/34/SM11), aerial sightings show a continuous distribution of Baird's beaked whales along the eastern coasts of Japan (Kasuya, 1971).

Seasonal changes in abundance do not give definite indications of migrations but suggest some northward movement along the eastern coast of Japan (Honshu and Hokkaido) from July–August to October–November.

4.3.2 Catches

Soviet catches of Baird's beaked whales at Kamchatka and the Kuril Islands from 1934 to 1964 add up to 143, while a total of 35 was taken off the coast of British Columbia between 1950 and 1966, and 14 were landed by a Californian fishery from 1959 to 1966 (Mitchell, 1975a). After the sub-committee had completed its deliberations, it was informed by Tillman that the Soviet NP forms contain data on pelagic take of *Berardius* in the North Pacific. The sub-committee did not have time to pursue this lead. No further catches have been reported for these fisheries. However, catches by land-based small-type whaling operations continue in Japanese coastal waters, where whaling for the *tsuchimbo* can be documented back to the early part of the 17th century in the Chiba prefecture (SC/34/SM11).

Catches by one Chiba company from 1815 to 1869 fluctuated widely, with an annual average of 9 whales. Catches virtually stopped after 1870, but some whales apparently were taken during the 1890s and later, particularly after the introduction of the first modern whaling vessel in 1907. Catches were small up to World War II (Omura *et al.*, 1955), and an average of 15 per year was recorded for 1941–43. The total catch through the period 1907–47 is estimated at about 600 on the basis of an assumed catch of about 15 per year (SC/34/SM11).

Small-type whaling expanded rapidly after World War II on the Japanese coasts. A licensing system was introduced in 1947, and the number of licensed small-type vessels hunting minke, Baird's beaked, short-finned pilot, killer and other medium or small-sized whales reached a maximum of 80 in 1950, and then decreased to an average of eight during the last ten years.

Japanese catches of Baird's beaked whales peaked at a total of 485 in 1952 and fell off to less than one tenth of this number in recent years. Average total catches per year through the post-war years are given for ten-year periods in Table 7, and available data on catch and effort in the coastal Japanese small-type whaling operations, with specified information on the exclusive fishery for Baird's beaked whale in the Chiba Prefecture, are given in Table 8.

Table 7

Average total annual landings of Baird's beaked whale by Japanese small-type coastal whalers, 1948–81 (SC/34/SM11)

Years	No. of whales
1948–57	217
1958–67	164
1968–77	71
1978–81	34
Average per 10 year period 1948–81	137

Table 8

Landings of Baird's beaked whales and other species by Japanese small-type coastal whalers, 1972–81 (SC/34/SM11; additional information supplied by Ohsumi)

	Total—coastal whaling			Chiba fishery	
		No. of whales			
Year	No. of vessels	Baird's beaked	Other species	No. of operating boats	No. of Baird's beaked
1972	9	86	452	3	86
1973	8[1]	32	620	2	30
1974	8[1]	32	437	2	32
1975	8[1]	46	431	3	39
1976	7	13	375	2	11
1977	7	44	256	2	28
1978	7	36	411	2	33
1979	9	28	410	3	24
1980	8	31	379	3	23
1981	8	39	374	—	—

[1] Included catches by one 200-ton experimental vessel:
1973 1 Baird's, 118 minke
1974 0 Baird's, 81 minke
1975 5 Baird's, 80 minke

The fishery is now mainly directed at minke whales, which constituted 83.6% of the total landings during the past ten years. Baird's beaked whales amount to 8.5%, and other species, mainly short-finned pilot whales but also a few killer whales and others, make up the remaining 7.8% of the total catches in 1972–81.

The recent decline of coastal catches in Japan up to 1973 when they levelled off (SC/34/SM11), is believed to have been caused by a reduction in the number of licensed small-type whaling vessels from 18 in 1966 to half this number in 1972, and a simultaneous shift of effort towards minke whales. The statistics show a nearly compensatory increase in catches of minke whales (SC/34/SM11).

Catches of beaked whales actually stopped in the previous area of highest catches at Tohoku Region on the Pacific coast of Honshu, while catches in the waters around Hokkaido were reduced to a very low level. These are now major fishing grounds for minke whales. At Chiba, however, the traditional fishery for beaked whales continued, although on a relatively low level with only 2–3 boats operating through the last decade (Table 8).

4.3.3 Life history and vital parameters

In a previous study, Omura *et al.* (1955) reported sexual maturity of males at body lengths of 9.7–10.2 m in males and 10.0–10.5 m in females. More recent estimates are 8.9–10.0 m in males and 9.9–10.4 m in females, and the length at 50% maturity now is estimated at 9.5 m and 9.9 m for males and females respectively (SC/34/SM11). Age at sexual maturity has been estimated at 9.0 years (Ohsumi, in press; Kasuya, 1977).

Data from a small sample of 11 females suggest an apparent pregnancy rate of about 50%, but the actual pregnancy rate is probably lower (SC/34/SM11), possibly about 25% (Ohsumi, in press). There may be bias due to selectivity in the catch.

The gestation period was found to be 17 months by Kasuya (1977) and has since been calculated to be 16.7 months (Ohsumi, in press). Body length at birth is estimated at 4.4 m, length at one year at 5.6 m and length at weaning at 8.6 m. It is therefore assumed that lactation lasts for more than one year.

Natural mortality has provisionally been deduced at 0.083 based on a comparative study (Ohsumi, 1979).

Some sexual segregation is indicated by the high proportion of males (about 80%) in catches in Japanese coastal waters (SC/34/SM11).

4.3.4 Status

No estimate of stock size is available for the total oceanic stock in the North Pacific, nor for the hypothetical stock of Baird's beaked whales in Japanese waters.

Total CPUE estimates for all operating licensed vessels for the past decade have been stable (Table 1, SC/34/SM11). However, the 'density distribution' of Baird's beaked whales, calculated as the number of whales sighted per hour of operation as reported by the whalers since 1977, indicate a definite increase through the last five years for both the Pacific Coast of Hokkaido and the Chiba area (SC/34/SM11). Ohsumi noted that operation time was recorded by each vessel at the time from the start of the search at sunrise until all work closed for the day, and included searching, waiting for whales to reappear after dives, chasing time and handling time. He also noted that sonar is not used in the Baird's beaked whale fishery.

It was pointed out that estimates of variance in the sighting data are needed before the short series of 'density distributions' can be used as indices of abundance. It was also noted that the rates of increase were too high to be simply due to an increase in stock abundance.

The change in sighting frequencies might also reflect a change in distributional behaviour. Ohsumi and Kasuya noted that the distribution of small cetaceans in Japanese coastal waters is related to oceanographic conditions. It is likely, therefore, that variations in sightings among years may have been caused by changes in the physical and related biological factors in the sea.

The sub-committee agreed that further studies were needed to establish any evidence for a sustained oceanographic change. It was also agreed that comparative analyses of previous CPUE data should be undertaken and that the history of the catch should be further documented.

An analysis of published catch-per-boat data was presented in SC/34/SM8. Assuming that boat efficiency increases faster than tonnage, this analysis asserts a decreasing abundance of Baird's beaked whales when boat efficiency is corrected by the cube of boat-tonnage.

Another underlying assumption is that the abundance of minke whales which are most extensively hunted in an allegedly mixed fishery, has remained constant. Ohsumi and Miyazaki, supported by evidence presented in SC/34/SM11 and SC/34/Mi16, pointed out the seasonal separation of operations in whaling for minke and Baird's beaked whales and noted that boat size did not affect efficiency in the fishery for beaked whales.

The sub-committee agreed that the analysis in SC/34/SM8 is based on faulty assumptions and should not be used in assessment of the stock. Fortom-Gouin noted that daily catch and effort records for the fishery are not available from IWS or in the Japanese Progress Reports.

4.3.5 Conclusions

The members of the sub-committee agreed on the following:

1. The limits of distribution of the population exploited by Japan are unknown. Although Baird's beaked whale occurs across the North Pacific, it is possible that the whales exploited by Japan comprise a discrete stock.
2. The original size of the population, its present size, and its level relative to initial size and MSY level are not known.
3. An average annual catch of about nine whales was taken over a period of 55 years in the 19th century (range 0–26).
4. Average annual catches in the 1950s of about 250 whales (average 242; range 186–322) were followed by a decline in catches during the 1960s and early 1970s to present levels of about 30 per year (average 33; range 13–46 over period 1973–81).
5. In one area off Chiba (Area D in SC/34/SM11, p. 17), the nominal catch per boat increased over the period 1947 to about 1974, and possibly declined from about 1975 onwards (SC/34/SM11, p. 23). The number of whales sighted per hour of operation in Areas D and B (off Southern Hokkaido) may have increased over the period 1977–81.
6. The sub-committee is uncertain about the validity of the measures of effort employed in SC/34/SM11, for several reasons: fluctuations in the number of vessels hunting Baird's beaked whales, changes in vessel-tonnage composition of the fleet, the operational nature of searching effort (involves waiting at the surface for long periods while whales are submerged), aggregating behaviour of the whales, a sharp change in sex ratio in the catch (SC/34/SM11, p. 24) and the high apparent rates of increase in CPUE measures (SC/34/SM11, p. 23).
7. The sub-committee is unable to recommend a classification for the stock. If the Commission should wish to establish a catch limit on the basis of recent catches, the catches in the last ten years are listed in

> Table 8 (the annual average for 1972–81 is 39 whales). The sub-committee believes that such catches over a short period would not seriously affect the stock, but that research should proceed to obtain the information necessary to assess the status of the stock (see Agenda Item 10).

Ohsumi noted that the studies proposed (Item 10) would require considerable time as well as funds. In order to justify such dual investment it would be necessary to go through the formal research proposal procedures stipulated by the Government of Japan. In addition, industry's financial committment is also indispensable. At this point it seems highly unlikely that the Government and industry would approve such committment without tacit assurance of the preservation of the whaling industry for a considerable period. Lastly, it should be pointed out that the efficiency of this type of study is very precarious unless a substantial whale catch is guaranteed.

4.5 Arnoux' beaked whale, *Berardius arnouxii*

No new information was available on this species.

5. REVIEW OF NEW INFORMATION ON OTHER EXPLOITED SMALL CETACEANS

Because of shortage of time due to major concentration on the pelagic dolphins and the beaked whales, the sub-committee only very briefly reviewed new information on other small cetaceans.

5.1 White whales

5.1.1 Distribution and abundance

Based on aerial surveys conducted in 1980–82, populations in the Okhotsk Sea in summer were estimated at 8,000 to 9,000, distributed at Sakhalin Bay and in the Amur River Estuary (6,000–7,000) and in Shelikov Bay (2,000) (SC/34/SM13). Methods used to calculate these population estimates were not described in sufficient detail to permit assessment of their reliability by the sub-committee. Results of aerial surveys in winter tentatively support earlier speculations (Kleinenberg *et al.*, 1964) that individuals in this stock winter in ice-covered areas of the Okhotsk Sea and respond in their local movements to ice edge shifts (SC/34/SM13).

Sightings data for Baffin Bay and Davis Strait were reported in SC/34/ProgRep Denmark. Kapel reported that papers analysing the data do exist, but they were not available to the sub-committee.

The isolated stock in the Gulf of St. Lawrence is now estimated to contain about 300 animals (SC/34/ProgRep Canada).

*5.1.2 Catches**

The recent catches of white whales by Canada, Denmark (Greenland), the USA and the USSR are summarised in Appendix 2. Details of takes by region or village are shown for Canada in Table 9 and the USA in SC/34/PS9 and Table 10. Brodie reported that the catch statistics for northern Quebec are incomplete. The sub-committee reviewed the partial record of takes in 1981 in waters of the USA and noted the existence at Point Lay (Icy Cape), Alaska, of an occasional drive fishery in which one to several hundred animals might be driven ashore and killed on a given drive. Fraker reported that other such drive fisheries likely exist in Alaska. Brodie reported that some of the US take may be from populations previously thought to be exploited mainly by Canadian Inuit. The sub-committee expressed concern about the minimum levels of these previously unreported takes in waters of the USA (reported catch is now greater than for Canada) and agreed that more information is required.

Table 9

Details of takes of white whales and narwhals in Canada in 1981 (partial list prepared by J. S. Loch, 20 May 1982 [SC/34/ProgRep Canada] updated by Brodie and Fraker). Does not include takes from northern Quebec (Ungava Bay)

Subdistrict	White whale	Narwhal
Baffin (villages)		
Arctic Bay	0	100
Broughton Island	0	50
Cape Dorset	1	0
Clyde River	0	37
Frobisher Bay	44	0
Grise Fiord	47	0
Hall Beach	5	17
Igloolik	60–80	36
Lake Harbour	16	0
Pangnirtung (Cumberland Sound)	45	44
Pond Inlet	0	82
Resolute Bay	8	0
Sanikiluaq	6	0
Subtotal	232–252	366
Keewatin		
Chesterfield Inlet	11	0
Churchill	1	—
Repulse Bay	52–56	29
Coral Harbour	8	6
Rankin Inlet	61	5
Eskimo Point	52	0
Whale Cove	22	0
Subtotal	207–211	40
Central		
Bathurst	—	—
Cambridge Bay	—	—
Pelly Bay	—	—
Spence Bay	28	—
Gjoa Haven	—	—
Coppermine	—	[c]
Holman Island	—	[c]
Subtotal	28	—
Inuvik		
Aklavik	35[a]–45[b]	[c]
Inuvik	52[a]–62[b]	[c]
Tuktoyaktuk	62[a]–105[b]	[c]
Subtotal	149[a]–212[b]	[c]
Grand total	616–703	406

[a] Number landed. [b] Total number killed (includes estimates of sinking loss). [c] Does not inhabit this area, according to Fraker.

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* Editor's note. The US National Marine Fisheries Service has informed us that a detailed review of the 1981 Alaska white whale fishery presented to it by the Alaska Department of Fish and Game in September 1982, revealed an estimated take of 182–237 animals, not the 614–649 value originally presented to the sub-committee. The revised catch figures by region or village are shown in square brackets in Table 10, after the values which were available to the sub-committee. The summary values in Appendix 2 have been similarly amended

Table 10

Details of preliminary catch data available for white whales in United States waters in 1981. [As indicated in the footnote to section 5.1.2 new information has been supplied by the US Marine Fisheries Service. The revised estimated takes are shown in square brackets and are also cited in Braham (in press).]

Region	Village	Reported catch	
North Coast	Barter Island	0[a]	[0]
Northwest Coast	Barrow	5[b]	[5]
	Wainwright	0[b]	[0]
	Point Lay	75–100[b]	[29–38]
	Point Hope	4–7[a]	[4–7]
	Kotzebue Sound	249[c]	[4]
	Escholtz Bay		[39]
Norton Sound	Yukon River	25–28[a]	—[e]
	St. Michael	11[a]	[11]
	Stebbins	10–20[a]	[10–20]
	Shaktoolik	7–15[a]	[7–15]
	Koyuk	21–25[a]	[21–25]
	Elim	3[a]	[3]
	Nome	1[a]	[1]
Kuskokwim		<100?[d]	—[e]
Bristol Bay		35–45[c]	[10–20]
Cook Inlet		?	[3–6]
	Estimated total:	<546–<609	[182–237]

[a] Table 2 in SC/34/PS9.

[b] Provided by Dronenburg

[c] J. J. Burns, Alaska Department of Fish and Game, Fairbanks, Alaska

[d] Reported by Leatherwood.

[e] The revised data give an estimated take of 25–28 for the 'Yukon–Kuskokwim deltas'.

5.1.3 Status

No new data were presented on the status of high Arctic stocks of white whales. The isolated stock in the Gulf of St. Lawrence is believed to be declining, for reasons poorly understood (SC/34/ProgRep Canada). SC/34/SM13 states that the Sea of Okhotsk stock(s) could sustain an annual take of about 1,000 individuals, 11.1 to 12.5% of the estimated total population. The sub-committee noted a view expressed that takes of 100 per year would be more appropriate. The population is not currently being exploited. The sub-committee noted that the latter level of take would be more in line with previous recommendations.

The sub-committee recalled its previous reviews of the Cumberland Sound stock, resulting in repeated recommendations that the stock be classified as a Protection Stock with a catch limit of 0 (*Rep. int. Whal. Commn* 30: 123–4; *Ibid.* 31: 150; *Ibid.* 32: 121–2), and noted with concern a quota of 40 and a take of 45 for that area in 1981 (SC/34/ProgRep Canada).

5.1.4 Recommendations

The sub-committee noted that research recommendations made in previous years have been acted on by the USSR and Canada. The research (reported in ProgReps and the SM series) includes studies of population size, productivity and exploitation in waters of the USSR and population size, discreteness, exploitation history and loss rates in Quebec, Hudson Strait, Northeast Hudson Bay, the Canadian High Arctic and West Greenland. The sub-committee noted, however, that takes in 1981 in Cumberland Sound, Eastern Hudson Bay and Ungava Bay (SC/34/ProgRep Canada) were high relative to the population size (*Rep. int. Whal. Commn* 32: 114) and therefore repeats the recommendation of last year for complete protection of these stocks (see Agenda Item 10.5). The sub-committee feels strongly that catch statistics should be collected by the USA and more complete statistics collected by Canada and reported to the IWC and that the USA should be urged to carry out assessment research (see Agenda Item 10.5).

Noting that studies of white whale and narwhal distribution in Baffin Bay and Davis Strait have been carried out by the consulting company LGL Ltd for the Arctic Pilot Project (Petro Canada) following recommendations by a Danish-Canadian working group, the sub-committee feels that the governmental representatives of the said working group should attempt to make reports of such studies available to future meetings of the Scientific Committee.

5.2 Narwhals

Information on sightings was reported in SC/34/ProgRep Denmark (Greenland) and by Leatherwood for Alaskan waters.

Recent catches of narwhals by Canada and Denmark (Greenland) are summarised in Appendix 2. Canadian takes by village or region are presented in Table 9.

No new information was available concerning loss rates or status of populations.

5.3 Killer whales

5.3.1 Distribution and abundance

A total of 9,000 killer whales was sighted from Soviet whaling ships in 1980 in the area from latitude 63° to the ice edge between longitudes 60°E and 141°40′E (SC/34/SM15). Zemsky reported that the statement in SC/34/SM15 that the 9,000 figure represented the size of the stock was a mistake of translation. The size of the stock was not estimated.

In 1981, Norway acted on the Committee's recommendation of last year that the killer whales along the Norwegian coast be censused. Based on reports of fishermen completing questionnaires (332 of 5,000 distributed) the minimum population of killer whales in Norwegian waters was estimated at 1,115 individuals (SC/34/SM4). Concentrations were noted in areas previously indicated to be important (Jonsgård and Lyshoel, 1970; Christensen, 1982).

Additional information on sightings is presented in SC/34/O 3, SC/34/O 24 (Andaman Sea), SC/34/ProgRep Brazil (N. Atlantic), SC/34/ProgRep Japan (S. Hemisphere) and SC/34 ProgRep New Zealand (N.Z. waters) and Spain.

5.3.2 Catches

The 1981 voluntary Norwegian national quota of 52 animals was assigned with no time limit. Thirteen animals were taken in 1981 including eight off Vestfjorden in January.

Live captures off Iceland from 1975 until 1981 are summarised under Agenda Item 6.

5.3.3 Vital rates

The sub-committee reviewed a report providing considerable detail on the composition of the catch of 906 whales by the USSR in the Antarctic in 1980 (SC/34/SM15). This was in response to a request by the Scientific Committee in 1981. Pregnancy rates indicated by the sample (41.76% of all taken) are consistent with those reported for killer whales taken in the Norwegian coastal fishery (Christensen, 1982). The sub-committee expressed concern, however, that both sets of figures were significantly higher than rates of production in population(s) monitored for many years by direct observation (Bigg, 1982; Balcomb *et al.*, 1982). Christensen noted, however, that the proportion of females pregnant in the catches is consistent with his observations of numbers of calves accompanying females (Christensen, 1982).

Zemsky reported that harpooners do select larger animals. Christensen noted that it is very difficult to harpoon killer whales because of their speed and evasive behaviour. This leaves open the possibility that slower animals may be harpooned selectively. Most members of the sub-committee felt there is uncertainty about the representativeness of the sample and agreed that the data presented would be difficult to interpret without information on possible bias from hunting practices and killer whale behaviour.

The sub-committee notes that SC/34/SM15 did not contain age data for the sample of 906 animals. Because of the importance of age-specific reproductive rates in modeling population dynamics and assessing status, the USSR is urged to age the sample and analyse the data.

5.4 Pilot whales

5.4.1 Distribution and abundance

Sightings of pilot whales were reported for the 1981/82 IDCR Cruise (SC/34/ProgRep Brazil); in SC/34/ProgReps New Zealand and Spain, and SC/34/O 3, O 5, and SC/34/Sp9.

5.4.2 Catches

Catches of pilot whales by Denmark and Japan are presented in Appendix 2. Takes known to have occurred in a US live-capture fishery were unreported. Records of takes by the Faroe Islands (Denmark) are reported by village in Appendix 5.

The sub-committee reviewed evidence of a presumably now defunct fishery that took short-finned pilot whales for bait in a shark fishery in the Gulf of Mexico, off the USA, prior to 1972 (Mundus and Wisner, 1971). The total size of the catches is unknown.

5.4.3 Vital rates

Information in SC/34/ProgRep Australia partly summarises research on *Globicephala macrorhynchus* off Japan. Two reports by Marsh and Kasuya will appear in *Rep. int. Whal. Commn* (special issue 6), the proceedings volume of the recent conference on cetacean reproduction (see SC/34/Rep 1 and its Annex).

5.5 Dall's porpoise

5.5.1 Abundance and identity of stocks

Based on sightings from Japanese salmon research vessels and US platforms-of-opportunity vessels, Dall's porpoise in the North Pacific is estimated to number 1.2 million to 1.7 million (these are point estimates—no measures of confidence are reported) (SC/34/ProgRep USA). Composition of the population(s) in the US Fishery Conservation Zone, as represented by the specimens examined from the catch, are 725 individuals of the *Phocoenoides dalli-dalli* type and 2 of the *P. dalli-truei* type (SC/34/ProgRep USA). Recently Japanese takes in coastal fisheries have been mostly of the *truei* type (SC/34/SM10).

5.5.2 Catches

Reported takes by Japan and the US are presented in Appendix 2. However, some members of the sub-committee noted that these figures represent only partial accounting. Incidental kills associated with Japanese salmon fishing in the Fishery Conservation Zone of the USA occurred at a rate of 0.18 porpoises per set observed, or an estimated 1,850 animals (95% confidence limits 1,493–2,206) (SC/34/ProgRep USA). Kills in other areas are not reported, and no estimate of incidental takes in this fishery is included in SC/34ProgRep Japan. The sub-committee urges that Japan and the USA report completely the takes of this species by all methods in all areas. Miyazaki reported that fuller statistics are available in the 1981 INPC Report.

5.6 Harbour Porpoise

The recent catches of harbour porpoises by Denmark (SC/34/ProgRep Denmark) and Japan (SC/34/ProgRep Japan; ProgRep USA; SC/34/SM10) are summarised in Appendix 2. Details of Greenlandic catches by district are presented in Appendix 6. Estimated takes by Turkey in the Black Sea fishery are discussed in Agenda Item 3.1. Known incidental takes along the US coasts were not reported in SC/34/ProgRep USA.

6. LIVE-CAPTURE FISHERIES

Data on live-capture fisheries for 1981 are fragmentary, and no document dealing with the subject was submitted to the meeting, nor did any of the ProgReps contain information.

Between 1975–81, the government of Iceland issued 14 permits for the taking of 56 killer whales. A total of 37 animals were captured. A total of 34 were taken in the 1975–80 period; 26 were exported, 6 released and 2 died (summarised below). Data were provided by Sigurjónsson (first two columns), Klinowska (1981 data) and M. Dahlheim, National Marine Laboratory, Seattle, Washington.

Year	No. of permits issued	Quota	Number captured	Exported	Released	Died
1975	1	2	1	–	–	1
1976	2	6	5	3	2	
1977	2	10	6	6	–	–
1978	4	14	11	6	3	2
1979	2	8	6	6	–	–
1980	1	8	5	5	–	–
1981	2	8	3	3	–	1
	14	56	37	29	5	4

Appendix 5 in Hoyt (1981) is entitled 'Live Capture Statistics for Killer Whales' and contains detailed records of the live-capture fishery in California and Washington, USA; British Columbia, Canada; Iceland; and Japan for the years 1961–80; the data are summarised below.

Area	No. captured	No. died[1]	No. kept[1]	No. escaped or released
California	1	0	1	0
Washington	223+	10	31	182+
British Columbia	52	1	25	26
Iceland	34+	—	28	6+
Japan	5+	—	5	—
Total	315+	11+	90	214+

[1] Incomplete.

7. NEW INFORMATION ON INTERACTIONS BETWEEN SMALL CETACEANS AND FISHERIES

7.1 Incidental take

Incidental takes are listed in Appendix 2. New information on incidental catch was reported from British waters, Spain and the North Pacific.

The sub-committee drew attention in 1981 to the incidental take of harbour porpoise in British waters. Brown reported that arrangements were recently made for District Fishery Inspectors to include reports of incidental catches of cetaceans in their monthly reports to the Inspector of Fisheries. Any reports received will be passed to SMRU for transmission to the IWC Scientific Committee.

Van Beek reported that the number of bottlenose dolphins incidentally taken west of the British Isles by Dutch trawlers was estimated at about 15 per year. This figure was based on a small inquiry in the fishery carried out by the Research Institute for Fisheries at Yjmuiden.

In Spain a minimum of 14 bottlenose dolphins was captured, mainly off the Mediterranean coast (SC/34/ProgRep Spain). No information was available on the type of fishery and gear used.

Miyazaki (SC/34/SM10) reported the number of dolphins caught incidentally by Japanese seine net, gill net, set net and long line fisheries in coastal waters and brought to ports for human consumption. The number was 2,340 animals, of 10 species, in the six years from 1976 to 1981. These catches are not separated from directed catches in SC/34/ProgRep Japan.

Leatherwood noted that the US government for several years has issued permits to the Republic of Korea, USSR, the Federal Republic of Germany and perhaps other countries to take marine mammals incidentally while fishing in the southern Bering Sea and northern North Pacific. The permits have authorized incidental takes of Dall's porpoise and harbour porpoise, but the takes under those permits have not been reported by the USA.

Kasuya and Brownell reported that incidental take of small cetaceans by the Japanese gill-net fishery for red squid in the northeastern North Pacific is known to have occurred but has not yet been reported in SC/34/ProgRep Japan.

Incidental take of harbour porpoise along the Alaskan and Californian coast was reported in the Report of the IUCN Workshop on Marine Mammal/Fishery Interactions (IUCN, 1981) but has not been included in the USA progress reports.

7.2 Direct conflicts

As reported previously bottlenose dolphins are reported to take hooked fish in a hand-line fishery in Hawaiian waters; in addition there are unverified reports of rough-toothed dolphins taking bait in a Hawaiian longline fishery (IUCN, 1981).

Collet (Appendix 3) reported new information on the conflict between dolphins and the French tuna troll fishery in the eastern North Atlantic. Dolphins are killed with hand harpoons to scare away other dolphins from the fishing area. Separate estimates of these kills were not available. She also reported that dolphins have been entirely protected by law in France since 1970, and a recent request from fishermen in Corsica for permission to use sound emitters to scare dolphins in net fisheries was rejected in 1982 by the Government.

7.3 Competition

The Japanese Government in 1981 launched a new five-year research project to study dolphin populations which interact with local fisheries in the Iki Island area. Results of the previous three-year investigations of methods to scare the dolphins away from the fishing area were published in 1981 in Japanese but not available to the sub-committee.

8. NEW INFORMATION ON EFFECTS OF POLLUTION AND INDUSTRIAL DEVELOPMENT

Decisions made last year on new formats for progress reports, cooperation with other bodies and the Resolution passed by the Commission have resulted in an increase in available information this year. The progress reports of Australia, Canada, Denmark, France, Spain and USA all contained material on small cetaceans. Clearly much work is underway, and the results of the new studies will help to clarify the situation of cetaceans in these matters. Unfortunately, many planned and reported studies still take no account of the effects of pollutants, and without this information it is impossible to assess the significance of reported levels. A further problem which needs attention in planning studies is selection of tissues for analysis. Comparison of different studies would be greatly facilitated if an agreed minimum list of required samples could be drawn up, with, for example, suggested locations on the animal for collection of samples. In this context, the initiatives of ICES and IOC in setting up special study groups are most welcome (IWC/34/28, IWC/34/11)

8.1 Pollution

SC/34/ProgRep France notes a study of skin necroses. Collet explained that most stranded common dolphins in France show numerous, small skin necroses, and this study is designed to investigate the matter. She also said that over the past two years stranded animals have been found with oil in the gastro-intestinal tract. Bottlenose and common dolphins are involved. For some years past similar oil residues have been found in the gastro-intestinal tract of stranded seals. This matter is also under investigation.

SC/34/O 14 discussed the possible implications of findings by Japanese workers (Fukushima and Kawi, 1981; Tanabe *et al.*, 1981) of significant transfer of PCBs from lactating striped dolphins to their calves. The first-born calf receives a larger part of the load of PCBs accumulated over the life of the mother through lactation. The sub-committee did not have time to discuss this work substantively.

SC/34/ProgRep Canada gives references to review papers on heavy metal and organochlorine concentrations in marine mammals in northern waters which were presented at recent meetings (Wagemann and Muir, 1981; Wagemann, Snow and Lutz, 1981) but the reports were not available to this meeting. Australia, Canada, France and Spain report continuing sampling programmes, much of the material from stranded animals, although harvested animals are also included.

It seems to be particularly important that monitoring is not confined to stranded animals, in view of the report that PCB levels in seals found dead were significantly higher and more variable than those in animals caught in nets or shot (IWC/34/11). It is also important that wherever possible anatomical investigations are made of sampled animals, where PCBs are concerned at least the reproductive tract should be examined. In seals and other mammals this structure appears to suffer damage from PCBs, although the exact relationship between observed abnormalities and PCB levels is not clear (IWC/34/11).

8.2 Industrial development

SC/34/ProgRep Denmark mentions investigations in connection with the Arctic Pilot Project (APP)[1]. Kapel added that in the early phase of the negotiations with the proponents (Petro Canada and others) the Danish representatives stressed that the general knowledge of marine mammals in Baffin Bay and Davis Strait was so poor that the possible adverse effects of the project could not be adequately assessed. In the past two or three years some studies have been carried out to address these problems, partly funded by APP, but the extent of these studies are far from sufficient in the opinion of the Danish representatives.

One particular issue is the question of the impact of noise emitted from the ice-breaking carriers. These problems were treated only superficially in the environmental impact statement originally submitted by the proponents, but was raised by Danish scientists in the Working Group established to look into environmental and technical problems relating to the suggested routes with passage through Greenland waters.

APP reacted by calling a workshop to discuss questions of noise and have initiated some studies (Anon, 1981). The results of these studies are, however, not sufficiently convincing to remove Danish doubts. Indeed, studies carried out by Danish consultants appear to support the opinion that noise could have an effect over large areas.

Fraker reported on the 1981 White Whale Monitoring Program in the Mackenzie Estuary (Fraker and Fraker, 1982). This is the tenth such annual study and besides reporting on the industrial activity, which appears to have had rather little major effect in general, this work has provided much information about the animals themselves and the hunting. A few short-term effects of activity are noted: noisy and/or moving vehicles, high numbers of vessel movements and long duration of stimuli do disturb animals, particularly where there is less space for escape, as in narrow ice leads.

9. OTHER BUSINESS

9.1 Research proposals

The sub-committee reviewed SC/34/RP 1–7. The research proposed in SC/34/RP1 has already been started by the US National Marine Fisheries Service. SC/34/RP4 was deemed to more directly concern the sub-committee on protected species, but the sub-committee does note that if data on struck-and-loss rates, or local catches for white whales and narwhals, are uncovered in the proposed study they would be of use in future meetings.

SC/34/RP5 was tendered in response to a request originating in last year's special meeting on killer whale populations and meeting of the sub-committee (SC/33/Rep 4). The sub-committee considered what would be the best use of DFL 12,000 donated to the IWC by the Nethelands for research on small cetaceans and decided, based on the conclusions of the killer whale meeting, that highest priority should be given to research on stock identity of killer whales. The sub-committee therefore strongly supports the proposal in principle. As submitted however, the proposal is not sufficiently detailed and should be returned for revision, along guidelines supplied by the Secretariat. The sub-committee notes that the proposal is for a one-month pilot study and that should the initial study prove successful, funding from some source would be required for continuation of the research.

The sub-committee does not support the remaining proposals (SC/34/RP2, 3, 6, and 7).

9.2 The 1983 meeting of the sub-committee

The group proposes to focus next year on status of populations of phocoenids, including those taken incidentally; on *Cephalorhynchus spp*; and on populations of small cetaceans involved in live-capture fisheries.

9.3 Publication of documents

The following documents were recommended for publication: SC/34/SM1, 2, 3, 5, 9, 10 (with revision), 11 (with revision), 14 (with revision) and 15 (with revision).

9.4 Sightings data from Oman

The Secretary is in receipt of a letter from the Director of Fisheries Research (and Commissioner for the IWC) of Oman with enclosures detailing small cetacean sightings by Oman Navy vessels from September 1981 to March 1982. These data may be obtained from the Secretary.

9.5 Errors in IWS

Members of the sub-committee found extensive errors in IWS LXXVIII (see Appendix 4).

10. RECOMMENDATIONS TO THE SCIENTIFIC COMMITTEE

10.1 The Black Sea

Because very large catches of dolphins and porpoise have been taken in proportion to estimated population sizes, because the populations are of unknown status but likely to be depleted, and because catches continue, the sub-committee urges the following actions:

(1) Improvement in harvest statistics is needed, in defined units, both to determine if the assumed value of centners as 100 kg is correct, if the levels reported correctly represent the fishery, and to determine species composition; we recommend that the IWC request Turkey's and FAO's

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[1] Transport of Liquid Natural Gas (LNG) from the Canadian High Arctic through Baffin Bay and Davis Strait in very large ice-breaking tankers.

assistance in obtaining original Turkish documents reporting catch levels, with translations, for the Scientific Committee's use.

(2) The series of aerial sighting surveys from 1967 to the present provides a possible basis for population size monitoring, and it is recommended that the data resulting from these surveys by the Soviet Union be presented to the Committee for analysis.

(3) Because the fishery is not well understood, and because little improvement in understanding of the fishery has occurred in the last several years, despite discussions in several forums (FAO, 1979; *FAO Fish Ser. No 5* [*Mammals in the Sea*]; recent IWC reports), we recommend that individuals in Turkey knowledgeable of the fishery and of the fishery statistics be invited to participate in the next Committee meeting.

(4) Because the dolphins feed on anchovies, the history and present status of the anchovy fisheries throughout the Black Sea should be described for Committee use. Additionally, the present catch of cetaceans in the Black Sea should be sampled for stomach contents; the available literature on the Black Sea dolphins should be reviewed on this point.

(5) Because the available biological studies on these cetaceans are quite old, the Turkish catch should be sampled in order to determine sex composition and the reproductive condition and length of the animals. The sub-committee urges that Turkey and FAO be approached on this matter.

10.2 Dolphin populations in the eastern tropical Pacific

Noting that the continuing incidental kill of dolphins in the purse-seine tuna fishery of the eastern tropical Pacific is a problem of international scope, the sub-committee makes the following recommendations:

(1) Member nations of the IWC should be urged to participate in the data collection programme of the Inter-American Tropical Tuna Commission. Members fishing on dolphins but not currently participating are Mexico, the Netherlands and Spain.

(2) Research into ways of reducing incidental mortality should continue, and crews of vessels of member nations of the IWC should be encouraged by member governments to participate in the seminars held by the IATTC.

(3) Since there is uncertainty about the assessments which have been made and consequently about the status of the stocks, the US should be urged to continue with plans for reassessment.

(4) Incidental catch statistics should be included in Progress Reports to the IWC as required by the Schedule. Mexico, especially, has a large and growing fleet and should be approached directly by the Secretary and urged to participate.

10.3 Striped dolphins in Japan

Noting that catches of striped dolphins have declined over a long period on the Izu Peninsula, that reproductive parameters have possibly changed in response to exploitation, but that available analyses of CPUE are not adequate to allow determination of the status of the stock, the sub-committee recommends that more detailed effort data and relevant information be retrieved, or collected, and analysed. The data should include if possible:

(a) effort in hours and days, by vessel, area, season and year;
(b) detailed oceanographic data;
(c) data on other major fisheries, in the area, especially that for squid;
(d) information on shifting of seasonal abundance (as well as effort and catch) year to year.

10.4 Bottlenose whales

10.4.1 North Atlantic

The status of research to obtain knowledge needed to assess the population of the northern bottlenose whale has not changed from the previous year, and the sub-committee recommends that the classification of the stock as a provisional Protection Stock should be continued.

10.4.2 North Pacific

The sub-committee recommends that if exploitation of Baird's beaked whales in the western North Pacific continues, an expanded programme of research be initiated to obtain the information necessary for determining the status of the stock. The programme should include, but not necessarily be limited to:

1. Refinement and re-analysis of CPUE data, including segregation of beaked whale and minke whale effort, inclusion of confidence intervals about the estimates, description of the searching and catching operations, and re-analysis of vessel tonnage effects. Other technological factors possibly relevant should be examined; these include acoustic equipment (type, when installed, and how used), speed, size and age of vessel, crew size and gun equipment.
2. Re-analysis of scouting vessel data to delineate range and estimate population density, including evaluation of sample size and seasonal effects, elimination of records likely to have been based on erroneous identifications, and presentation of data on miles of effort and actual sightings (including school sizes), by 5° block or smaller stratum if possible.
3. Additional research to determine the identity and range of the stock(s). Potential methods include tagging (on the grounds and in adjacent pelagic areas to the east and north—the latter by scouting vessels) and aerial survey.
4. Investigation of population dynamics based on analysis of samples and data from the fishery, on field observations (including analysis of aerial photographs) of age and sex structures of schools and the population, and on comparative studies of other, related and ecologically similar species.

Japan should be urged to provide the results of items 1 and 2 to the next meeting of the Scientific Committee.

10.5 White whales and narwhals

(1) Noting that for waters of the USA there continue to be very few data on population size, discreteness and vital rates and incomplete data on takes and total removals, the sub-committee recommends that the government of the USA be encouraged to initiate appropriate field studies, submit more complete white whale statistics, and summarise available survey data on these whales.

(2) Noting the quota of 40 set for the Cumberland Sound population of white whales and the landed take of 45 in 1981, the sub-committee again this year recommends that Canada be urged to afford complete protection to this severely depleted population. The same applies to the Eastern Hudson Bay and Ungava Bay stocks.

10.6 Statistics

The sub-committee repeats its recommendation of previous years that members be urged to collect and submit full statistics as detailed in 1980 (*Rep. int. Whal. Commn* 30: 124), including statistics for incidental catch and live captures. As statistics for considerable catches of white whales in Alaska have not been completely collected and reported by the USA, the Secretary should contact the USA and urge that such be done.

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THE NORTHERN ANCHOVY SPAWNING BIOMASS FOR THE 1982-83 CALIFORNIA FISHING SEASON

SUSAN J. PICQUELLE AND ROGER P. HEWITT
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038

ABSTRACT

The 1982 equivalent larval census estimate of the spawning biomass of the northern anchovy (*Engraulis mordax*) central subpopulation is 1,866,000 MT (2,060,000 short tons). This estimate is based on data gathered by an egg production survey conducted from January 18 to March 9, 1982. The abundance of larvae is projected from the daily production of eggs and the subsequent mortality of eggs and larvae. This equivalent larval census estimate will be the basis of the anchovy fishery optimum yield (OY) for 1982-83.

The egg production method estimate of anchovy spawning biomass is 378,000 MT (417,000 short tons). This is based on a production of 12.30×10^{12} eggs/day and a population (males and females) fecundity of 3.253×10^7 eggs/day/MT. The standard error of the egg production method estimate is 97,200 MT, for a coefficient of variation of 25.7%.

In 1982 the central subpopulation of northern anchovy was geographically distributed in the inshore portion of the Southern California Bight, from the Santa Barbara Channel Islands to northern Baja California. A smaller group was detected between Monterey and San Francisco Bays.

RESUMEN

La biomasa de la puesta en la población de *Engraulis mordax* de la zona central de California, fué de 1.866,000 Toneladas métricas durante 1982, estimación basada en la equivalencia del censo larval. Esta estimación está basada en los datos correspondientes a las exploraciones que desde el 18 de Enero al 9 de Marzo de 1982 se llevaron a cabo para determinar la producción de huevos en la región. La abundancia de larvas se calcula considerando la producción diaria de huevos y la mortalidad de huevos y larvas. Estas estimaciones equivalentes del censo larval serán la base para determinar el rendimiento que se podrá obtener en la pesquería de anchoa durante el período de 1982-83.

La producción de huevos como método para estimar la biomasa de la puesta de la anchoa resulta de 376,000 Toneladas métricas. Esto se basa en una producción de 12.30×10^{12} huevos diarios y una poblacion (machos y hembras) con fecundidad de 3.253×10^7 Toneladas métricas de huevos diarios. El error normal de las estimaciones por el método de producción de huevos es de 97,200 Toneladas métricas para un coeficiente de variación de 25.7%.

En 1982 la población de anchoa en la zona central de California estaba distribuida por la franja costera del seno del sur de California, desde las islas del Canal de Santa Bárbara, hasta el norte de Baja California. Un grupo de menor importancia se observó entre las Bahías de Monterrey y San Francisco.

INTRODUCTION

The biomass of the central subpopulation of northern anchovy (*Engraulis mordax*) has been assessed periodically using three independent methods: larval census (Smith 1972; Stauffer and Parker 1980; Stauffer 1980; Stauffer and Picquelle 1981); sonar mapping (Smith 1970; Mais 1974; Hewitt et al. 1976); and egg production (Parker 1980; Stauffer and Picquelle[1]). The anchovy management plan adopted by the Pacific Fishery Management Council (PFMC 1978) specifies that harvest quotas will be established by an optimum yield formula based on annual estimates of spawning biomass. Because of technical complexities in converting acoustic returns to fish biomass, the sonar mapping method is most useful for describing the disposition of adult schools. The egg production method is an improvement over the larval census method because it does not require multiple surveys and because it measures and incorporates variability in adult reproductive output. However, the optimum yield (OY) formula was developed based on larval census biomass estimates. The alternative estimation methods mentioned above produce estimates that consistently differ in magnitude from larval census estimates. Consequently, use of one of these estimates would systematically alter the optimum yields calculated from the larval-census-based formula. In order to avoid this

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[1] Stauffer, G. D., and S. J. Picquelle. MS. Egg production estimates of spawning biomass of the northern anchovy, *Engraulis mordax*, for 1980 and 1981. Southwest Fisheries Center, La Jolla, California.

problem, the PFMC has interpreted the OY formula to require a "larval census equivalent" spawning biomass estimate.

The Scientific and Statistical Committee of the PFMC reviewed egg production and larval census surveys conducted in 1979 and 1980, and recommended that replicate egg production surveys, concurrent with a larval census survey, be conducted in 1981. These were successfully accomplished, and the harvest quotas continued to be established using larval census estimates of biomass. In 1982 the National Marine Fisheries Service, in cooperation with the California Department of Fish and Game, conducted only an egg production survey. This report describes the survey results, the egg production estimate of biomass, and the equivalent larval census estimate of biomass.

The egg production method defines the spawning biomass as the quotient of the daily production of eggs in the sea and the daily fecundity (per ton of spawners) of the population (Parker 1980). The larval census method defines the spawning biomass as proportional to the average standing stock of larvae summed over four quarters of the year, and assumes constant reproductive output (per ton of spawners) and constant survival of the young. The proportionality constant was defined from a regression of sardine biomass on sardine larvae and assumes a relative fecundity between anchovy and sardine (Smith 1972).

No larval census was conducted in 1982; however, an equivalent larval census can be estimated by measuring larval mortality and projecting the number of larvae resulting from the measured egg production.

DESCRIPTION OF SURVEY

The 1982 egg production survey for the central subpopulation of the northern anchovy was conducted on board NOAA ship *David Starr Jordan* and F/V *Oregon Beaver* during the period January 18 through March 9, 1982. (For detailed descriptions of operations, see the respective cruise reports on file at the Southwest Fisheries Center, La Jolla, California, and California Department of Fish and Game, Long Beach, California.) A total of 992 egg samples was obtained on the *Jordan* using a small-mesh plankton net retrieved vertically from 70 m (Figure 1); adults were sampled on the *Beaver* and the *Jordan* with 187 midwater trawls (Figure 2); and the disposition of adult schools was described by sonar operated aboard the *Beaver* (Figure 3). In addition, the larvae were sampled with the 505-micrometer mesh bongo plankton net used for the larval census method. These samples are used to determine the posthatch survival of the larvae. Sea temperature, salinity, and weather observations were also recorded.

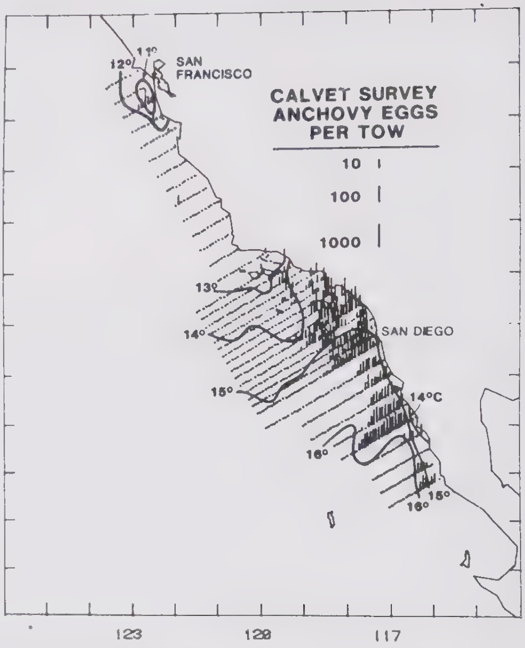

Figure 1. Geographic distribution of anchovy eggs in 1982. Spawning did not occur in cold water southeast of Point Conception or immediately adjacent to the northern Baja California coastline; some spawning was evident between Monterey and San Francisco bays.

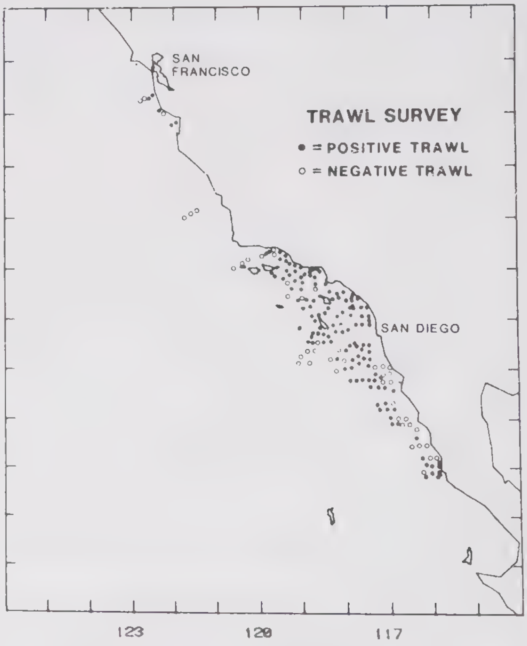

Figure 2. Geographic distribution of trawl sampling effort and trawls that caught adult anchovy (positive trawls). The distribution of adults matched the distribution of eggs (Figure 1).

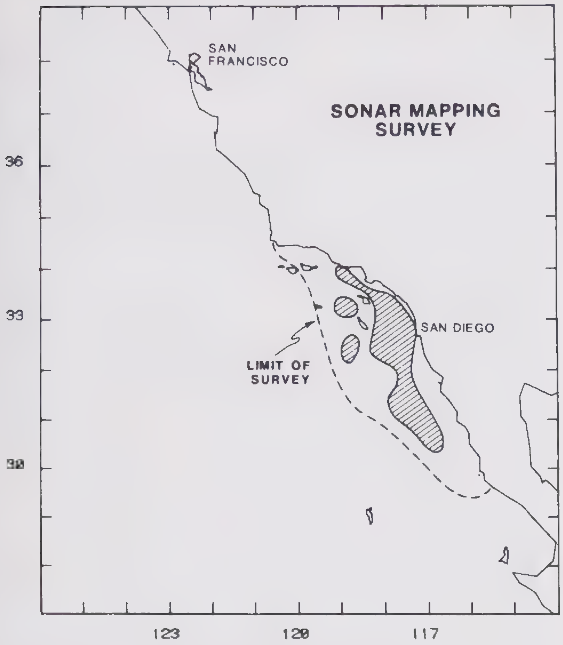

Figure 3. Geographic areas of heaviest anchovy concentration as mapped by sonar (K. Mais, CDF&G). The general distribution matches those of eggs and adults obtained by direct sampling.

Anchovy eggs were distributed along the northern Baja California coast and in the Southern California Bight as far north as the Santa Barbara Channel Islands (Figure 1). As in previous years, the geographic pattern of spawning was correlated with the pattern of surface temperature isotherms (Lasker et al. 1981). Spawning did not occur in water colder than 14°C south of Point Conception, although this is not considered a lethal temperature. Cold water was observed as a large plume extending southeastward from Point Conception into the Southern California Bight and immediately adjacent to the northern Baja California coastline (Figure 1). A much smaller area of spawning was sampled between Monterey and San Francisco Bays in 11-12°C water.

The geographic distribution of positive trawl samples agrees with the distribution of eggs (Figure 2). Adult fish were caught in the Southern California Bight, along the northern Baja California coast, and between Monterey and San Francisco. Adults were not caught in trawls taken in the Santa Barbara Channel and immediately adjacent to the northern Baja California coastline.

The geographic distribution of fish schools as detected by sonar agrees with the distribution of eggs and positive trawls (Figure 3). The area of heaviest anchovy concentration extends along the northern Baja California coastline (approximately 50 km offshore) and into the inshore portion of the Southern California Bight as far north as the Santa Barbara Channel Islands. Two smaller areas of heavy concentration were mapped in the offshore portion of the Southern California Bight.

In summary, northern anchovy, in the spring of 1982, were distributed continuously in the Southern California Bight from the Santa Barbara Channel Islands south to Cape Colnett. A second group was distributed between Monterey and San Francisco bays. In both groups fish were spawning, thus facilitating the use of reproductive surveys to estimate adult biomass.

EGG PRODUCTION ESTIMATE

Estimation Equation

The egg production estimate of anchovy spawning biomass, derived by Parker (1980) and modified by Stauffer and Picquelle (1980), is

$$B = P_o A \frac{k\,W}{R\,F\,S} \tag{1}$$

where B = spawning biomass (MT),

P_o = daily egg production, number of eggs produced per 0.05 meter^2,

W = average weight of mature females (grams),

R = sex ratio, fraction of population that are female, by weight (grams),

F = batch fecundity, number of eggs spawned per mature female per batch,

S = fraction of mature females spawning per day,

A = total area of survey (0.05 meter^2 units),

k = conversion factor for grams to metric tons.

An approximate sample variance for the egg production spawning biomass estimator, derived from the delta method (Seber 1973), is a function of the sample variance and covariance of the parameters

$$\begin{aligned}\mathrm{Var}\,(B) \cong B^2 \times \\ \Big\{ \frac{\mathrm{Var}\,(P_o)}{P_o^2} + \frac{\mathrm{Var}\,(W)}{W^2} + \frac{\mathrm{Var}\,(R)}{R^2} + \frac{\mathrm{Var}\,(F)}{F^2} + \frac{\mathrm{Var}\,(S)}{S^2} + \\ 2\Big[\frac{\mathrm{Cov}\,(P_oW)}{P_oW} - \frac{\mathrm{Cov}\,(P_oR)}{P_oR} - \frac{\mathrm{Cov}\,(P_oF)}{P_oF} - \frac{\mathrm{Cov}\,(P_oS)}{P_oS} - \frac{\mathrm{Cov}\,(WR)}{WR} - \\ \frac{\mathrm{Cov}\,(WF)}{WF} - \frac{\mathrm{Cov}\,(WS)}{WS} + \frac{\mathrm{Cov}\,(RF)}{RF} + \frac{\mathrm{Cov}\,(RS)}{RS} + \frac{\mathrm{Cov}\,(FS)}{FS} \Big] \Big\}\end{aligned} \tag{2}$$

Daily Production of Eggs in the Sea

The parameter P_o, the daily production of eggs in the sea, is the number of eggs spawned per night, per unit area, averaged over the range and duration of the survey. An ichthyoplankton survey is used to sample anchovy eggs to provide data on the density of the eggs by age. An exponential mortality model is then fit to the data, and the time-zero intercept of the fitted function is the estimate of egg production.

The sampling design of the survey is two-stage sampling with postsurvey stratification. The first stage is a systematic sample of block areas. The total area of the survey is divided into 4 × 20- (or 4 × 10-)nm blocks. The second stage is the selection of a 0.05-m^2 sampling unit in the center of the block (Stauffer and Picquelle[2]). This sampling design assumes that the distribution of eggs within one block is independent of the distribution within adjacent blocks. This assumption is based on experimental data showing that 4 miles is sufficient distance to ensure a negligible autocorrelation (P. Smith, pers. comm.). Advantages of this sampling plan are convenient and efficient use of ship time, even coverage of the total sample area, and improved precision of abundance estimates by maximizing the heterogeneity between adjacent sampling units (Jessen 1978).

Because of time and budget constraints, the sampling intensity was decreased in regions where fewer eggs were expected to be found. In the two 1981 surveys and the 1980 survey, the majority of the anchovy population was found in the Southern California Bight; a narrow band of eggs was typically found off Baja California; and very few eggs were collected off the central California coast. Therefore, the sampling fraction in the bight is increased to one sample per 4 × 10-nm block; elsewhere there is one sample per 4 × 20-nm block. To compensate for the uneven sampling intensity, each station is assigned a weight, w_{ij}, that is proportional to the relative area that the *j*th station represents in the *i*th stratum.

The total survey area is divided into two strata in order to reduce the variability about the egg abundance estimates. The geographic area of the survey is specified without knowing the actual area that the anchovy stock is currently occupying. Therefore, a portion of the surveyed area is beyond the range of the stock, contributing a large number of zero stations, which potentially inflates variance estimates. After the data are examined, a boundary for the current anchovy habitat can be drawn. The boundary is determined by following each line seaward until the last positive tow was taken. Thus all stations seaward of the boundary are zero, and all positive stations are shoreward of the boundary, along with many imbedded zero stations. The area within the boundary is allocated to stratum 1, and the area outside the boundary is put into stratum 0.

	Stratum 1	*Stratum 0*	*Total*
Area (nm^2)	24,190	35,039	59,229
Number of samples	396	596	992

Because the strata can be defined only after the data are collected, this technique is called postsurvey stratification. The area of each stratum, A_i, is not predetermined, so A_i is a random variable, and all variance estimates must be adjusted to include this source of variation (Jessen 1978).

The anchovy eggs from each sample are counted and staged according to the degree of embryonic development. The eggs are then classified into one-day age intervals based on the time of collection, surface water temperature, developmental stage, and laboratory-determined development rates. The ages are then further refined by adding the portion of a day that has elapsed between 2200 (the assumed time of spawning[3]) and the time of collection. This aging procedure is facilitated by the fact that eggs in a particular sample are either spawned on the same evening, or are separated by one-day increments, thus making it easier to separate the modes of egg abundance over stages into one-day age groups. Sea-surface temperatures for the majority of the cruise ranged between 13° and 17°C with an egg-weighted average of 14.9°C. At this temperature, eggs begin to hatch after 2.91 days. Eggs less than 2.67 days old were used in the analysis.

The daily production of eggs, P_o, and its variance are then estimated by regressing the counts of eggs on their age, using the exponential mortality model:

$$P_{ijk} = P_{oi} e^{-Zt_{ijk}} + \varepsilon_{ijk} \qquad (3)$$

where P_{ijk} is the number of eggs in the *k*th day age category from the *j*th station in the *i*th stratum; t_{ijk} is the age in days measured as the elapsed time from the time of spawn for the *k*th day category eggs to the time of sampling of the *j*th station in the *i*th stratum; P_{oi} is the daily production of eggs per unit area (0.05 m^2) in stratum *i; Z* is the daily rate of instantaneous egg mortality; and ϵ_{ijk} is the additive error term. This model assumes that all eggs are spawned and fertilized each day at time 2200, and eggs have a constant positive rate of instantaneous mortality[4].

The mortality function (equation [3]) is fit to the data by regressing the aged egg counts $\{P_{ijk}\}$ on their age $\{t_{ijk}\}$ for stratum 1 with a weighted nonlinear

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[2] See footnote 1 on page 16

[3] See footnote 1 on page 16

[4] See footnote 1

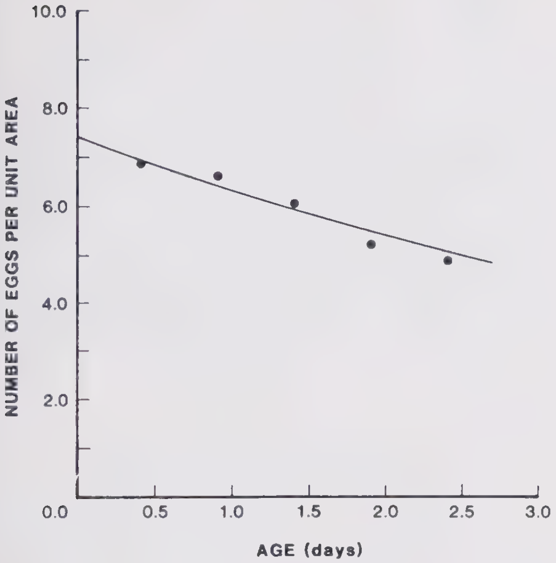

Figure 4. Mean egg production per 12-hour interval for stratum 1 is plotted against age in days. The exponential mortality model was estimated by regressing the individual egg counts on age.

least squares routine using a pseudo-Gauss-Newton algorithm (Dixon and Brown 1979). The individual weighting factors are the station area weights, $\{w_{ij}\}$. The resulting estimate of P_{oI} is 7.40 eggs per day per 0.05 m^2, and Z is 0.158 per day with variances 1.25 and 0.0110, respectively. A plot of the mean egg production per 12-hour interval and the estimated regression for stratum 1 are shown in Figure 4.

The final stratified estimate of P_o is the weighted average of the two strata where the strata weights u_i are proportional to A_i, the area of the ith stratum. P_{oi} for stratum 0 is zero by definition, thus:

$$u_i = \frac{A_i}{A_I + A_O}$$

$$P_o = u_I P_{oI} + u_O P_{oO} = u_I P_{oI}, \qquad (4)$$

and the variance, adjusted for postsurvey stratification (Jessen 1978), is

$$\widehat{\text{Var}}(P_o) = (1 + \frac{1}{n}) \left[\sum_{i=1}^{2} u_i \, (\widehat{\text{Var}}\,(P_{oi}) \right] \qquad (5)$$

where n is the total number of observations = 992; $\widehat{\text{Var}}\,(P_{o1}) = 1.25$ is estimated from the regression (3) for stratum 1, and; $\widehat{\text{Var}}(P_{o0}) = 0$ by definition.

The stratified estimate of P_o is 3.023 eggs per day per 0.05 m^2 for the entire survey area, with an estimated variance of 0.5119 and coefficient of variation of 23.67%. This estimate of P_o applies over the 59,299-nm^2 area of the survey ($A = 4.068 \times 10^{12}$ area units of 0.05 m^2 each).

Adult Parameters W, F, S, *and* R

The parameters W, F, S, and R are estimated from samples of adult anchovies collected by the midwater trawl survey. The sampling design consists of three stages: (1) placement of trawl stations, (2) trawl catch, and (3) subsample of fish. The statistical technique of judgment sampling is used in selecting the location for the trawls in order to achieve a high proportion of positive trawls. Station locations were selected where concentrations of anchovies were detected by the occurrence of anchovy eggs or larvae in the plankton samples, and the presence of apparent schools on the sonar (Figures 1, 2, and 3). Because more stations are selected where heavy concentrations of anchovies are suspected, the sample design follows the precepts of probability sampling (Cochran 1963).

One trawl is taken at each selected location, and the trawl catch is assumed to be a random sample of fish at the station. Each station is given equal weight by subsampling an equal number of fish from each trawl, m^*. This is appropriate if the probability of choosing a station is exactly proportional to the number of anchovies at the station; however, these probabilities are impossible to enumerate, so that the actual sampling design is only an approximation of the ideal design (judgment sampling rather than probability sampling). If the trawl catch size were a good measure of the abundance of fish at the station, this information could be used to improve the approximation of the ideal sample design. However, trawl catch size and abundance of fish are unrelated for anchovies; catch size depends more on the depth of the school, the avoidance of the net by the fish, and luck. This conclusion is supported by the historical lack of agreement between trawl catch size and the factors that indicate concentrations of anchovies (sonar detection, eggs and larvae in plankton samples).

Even though equal subsample sizes are attempted, they are not always attainable: the catch may have few mature females, or the catch may be extremely small. In these cases the stations should receive less weight to compensate for the error in judgment sampling; if there are few mature females in the catch then it is assumed that there are few mature females at the station, and if the catch is very small then it is assumed that the actual number of anchovies at the station is relatively small. Thus, each station is given a weight of the relative subsample size.

The estimates and variances, ($\bar{y}$) and var($\bar{y}$), of the four parameters—*W*, *R*, *F*, and *S*—are the weighted sample mean and sample variance (Cochran 1963)

$$\bar{\bar{y}} = \sum_{i=1}^{n} \left(\frac{m_i}{n\bar{m}}\right) \bar{y}_i \tag{6}$$

$$\widehat{\mathrm{Var}}\,(\bar{\bar{y}}) = \frac{\sum_{i=1}^{n} \left(\frac{m_i}{\bar{m}}\right)^2 (\bar{y}_i - \bar{\bar{y}})^2}{n(n-1)} \tag{7}$$

where m_i is the number of fish subsampled from the *i*th trawl, $\bar{m}$ is the average number of fish subsampled per trawl, *n* is the number of positive trawls, y_{ij} is the observed value for the *j*th fish in the *i*th trawl, and $\bar{y}_i = \sum_j^{m_i} y_{ij}/m_i$ is the average for the *i*th trawl.

The method described by equations (6) and (7) is used in the succeeding sections to estimate parameters *W*, *F*, *S*, and *R* and their respective variances.

Average Female Weight

The average female weight, *W*, is calculated as the weighted average of W_{ij}, the weight of the *j*th mature female from trawl *i*, using equation (6). The weight of females with hydrated eggs in their ovaries is temporarily inflated because of water retention, therefore their weight is adjusted using the regression of whole-body weight on ovary-free weight estimated from females that do not have hydrated eggs,

$$\hat{W}_{ij} = -0.0701 + 1.06\, W_{ij}^{*} \tag{8}$$

where W_{ij}^{*} is the ovary-free weight; the regression has an $r^2 = 99.6\%$. The desired subsample size is $m^* = 15$ mature females. The estimated average female weight is 18.83 g with a variance of 0.1319 (equation [7]) and coefficient of variation of 1.93%. The mode of the frequency distribution of $\bar{W}_i$, the average weight of mature female anchovies in the *i*th trawl, is at 19 g (Figure 5).

Batch Fecundity

For the estimate of batch fecundity, *F*, the individual observations, F_{ij}, are not observed directly but are estimated from a relationship between batch fecundity and ovary-free weight. This relationship is estimated from a sample of 109 hydrated females that were collected over the duration of the cruise. These hydrated females have a distribution of adjusted weights (equation [8]) similar to the weight distribution of females for the whole cruise (Figure 6). A linear regression of fecundity on weight was selected because the fitted exponent for the power function was not significantly different from one, indicating that any curvature present in the data is

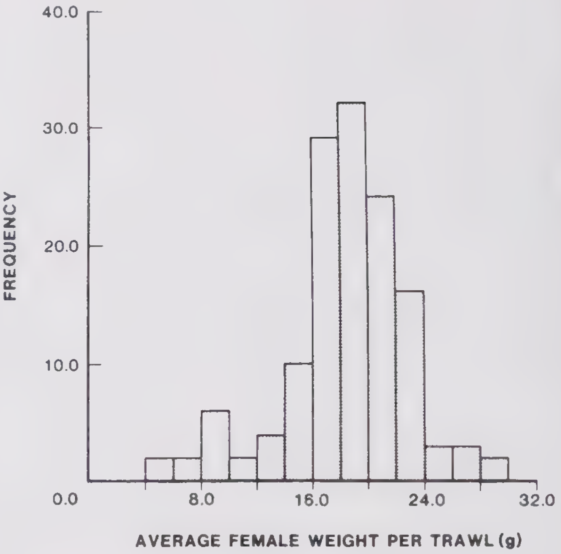

Figure 5. The frequency distribution of the average weight of mature females per trawl.

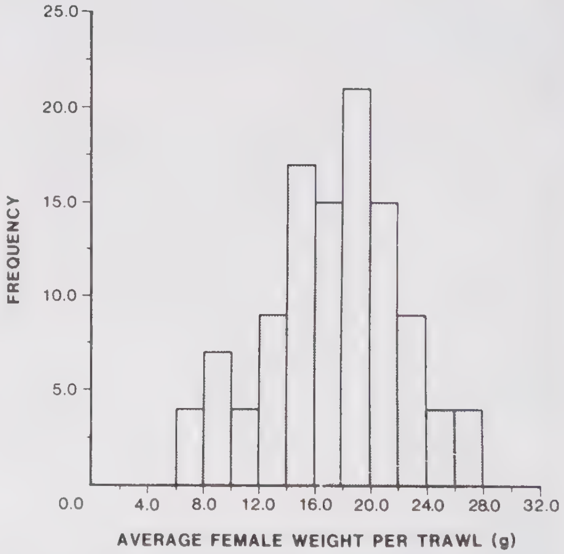

Figure 6. The frequency distribution of whole body weights for the hydrated females used in regression (9). The weights of the hydrated females were adjusted to nonhydrated weights using regression (8). The frequency distribution of adjusted weights is similar to that of the average weights of mature females (Figure 5).

very slight. The selected regression model is

$$\hat{F}_{ij} = -179.7 + 617.2\, W_{ij}^{*} \tag{9}$$

with an $r_2 = 52.4\%$ (Figure 7).

Based on this regression, the F_{ij} are estimated for each of the $m^* = 15$ mature females from each trawl. Estimated average batch fecundity is 10845 (equation [6]), with a variance of 171730 (equation [10]) and coefficient of variation of 3.82%. Because the trawl averages ($\bar{F}_i$) are not based on actual observations, but are estimates with their own variance, the variance estimate for F includes this additional source of variation (Draper and Smith 1966):

$$\widehat{\mathrm{Var}}(\bar{\bar{F}}) = \frac{\sum_{i=1}^{n} \left(\frac{m_i}{\bar{\bar{m}}}\right)^2 \left[\frac{(\bar{F}_i - \bar{\bar{F}})^2}{n-1} + \frac{S_h^2}{109} + (\bar{W}_i^* - \bar{W}_h^*)^2\, \widehat{\mathrm{Var}(b)}\right]}{n} \tag{10}$$

where $S_h{}^2 = 6658675$ is the variance about the regression (9); $\bar{W}_i{}^*$ is the average ovary-free weight for the ith trawl; $\bar{W}_h{}^* = 16.54$ is the average ovary-free weight for the 109 hydrated females; $\hat{\mathrm{Var}}(b) = 3172$ is the variance of the slope of regression (9); and $n = 135$ positive trawls.

Specific fecundity, expressed as eggs per gram of whole-body weight, is similar to those observed in 1981.

Year	1980	1981	1981	1982
Survey	8003/4	8102	8104	8202
Mean weight (g)	17.4	13.4	16.2	18.8
Eggs/gram	444.4	623.0	546.0	575.9

Spawning Fraction

Spawning fraction, S, is estimated from $m^* = 15$ mature females, and $S_{ij}^{l} = 1$ if the ovary of the jth mature female in the ith trawl is classified as having day-1 postovulatory follicles (day-1 spawners), and $S_{ij}^{l} = 0$ otherwise (see Hunter and Macewicz 1980 for histological definition of day-1 and day-0 spawners). Thus $\bar{S}_i^{l}$ is the proportion of mature females in the ith trawl that are in the day-1 spawning category (S^1).

Another measure of spawning activity is the proportion of mature females that are classified as day-0 spawners, S^0. In past surveys, it has been suspected that the proportion of day-0 females is a biased estimate because of oversampling of females that spawn on the night of capture. This was indicated by a large discrepancy between S^1 and S^0, with the deviation between these two measures reaching a maximum during the peak hours of spawning. There was also a co-occurrence of high values of $\bar{S}_i^{0}$ and low values for sex ratios for trawls taken during these hours, which suggested that males and day-0 spawning females segregate out from other females at the peak hours of spawning at a depth where they are more vulnerable to the midwater trawl[5]. In previous surveys, m_i was adjusted by assuming that the actual number of day-0 females is the same as the observed number of day-1 females.

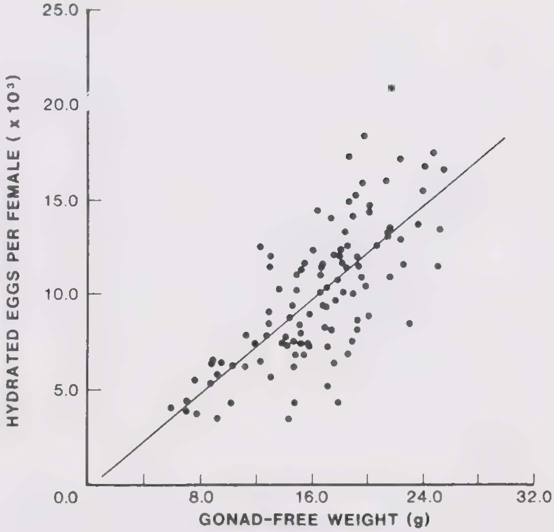

Figure 7. Batch fecundity regressed on ovary-free weight of 109 hydrated females using a linear model (equation [9]).

The apparent oversampling of day-0 females was reduced in this year's data; this may have been due to a slight change in the trawl gear. The difference between S^1 and S^0 is still greatest during the peak spawning time 2200-2259 (Figure 8), and there is still a dip in the sex ratio over the time 2000-2259 (Figure 9), but the discrepancy is very small relative to past years. In fact, the values of S^1 and S^0, 0.120 and 0.127, respectively, are not significantly different from each other. Thus, we concluded that day-0 spawning females were not oversampled this year. Hence, m_i is not adjusted and is simply the number of mature females in the ith trawl. The estimate of spawning fraction is 0.120 (equation [6]) with variance $= 9.47 \times 10^{-5}$ (equation [7]) and coefficient of variation $= 8.13\%$.

Sex Ratio

The parameter R, sex ratio, is the fraction of females in the anchovy stock based on fish weight.

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[5] See footnote 1 on page 16

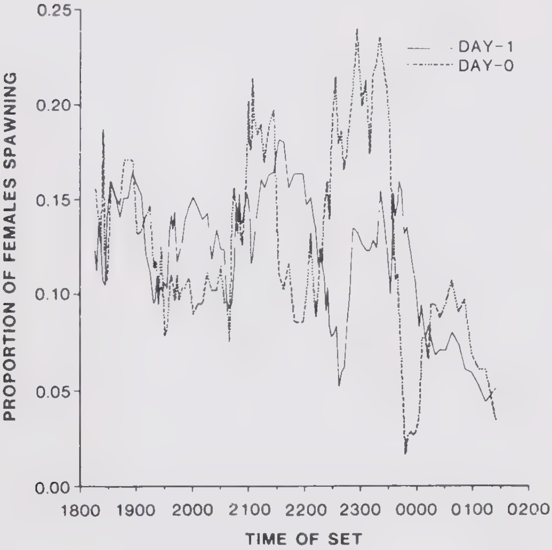

Figure 8. The running averages for S^0 (day-0 spawning fraction) and for S^1 (day-1 spawning fraction) plotted against the time of trawl. The running averages are based on 10 observations. The discrepancy between S^0 an S^1 is largest during the time interval 2200-2259, the peak time of spawning.

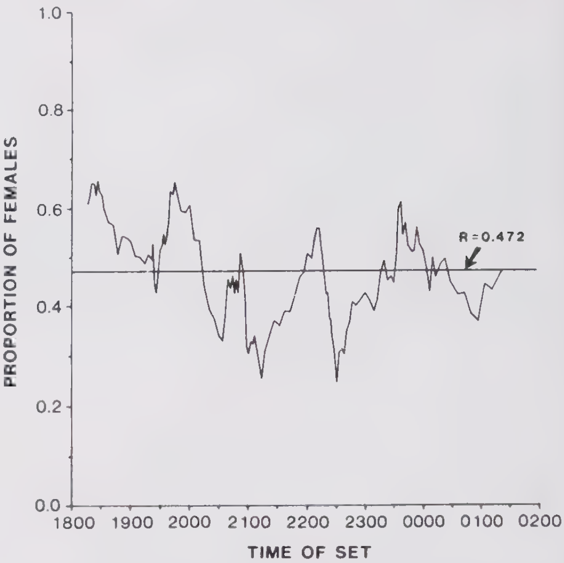

Figure 9. The changes of observed sex ratio with time. The running average for sex ratio is based on 10 observations. The horizontal line is the estimated mean sex ratio.

TABLE 1
Estimates of Egg Production Parameters and Spawning Biomass for 1982

Parameter	Symbol	Mean	Variance	Coefficient of Variation
Egg production (eggs/0.05 m^2-day)	P_0	3.023	0.5119	0.237
Area of survey (0.05 m^2 units)	A	4.068×10^{12}	—	—
Average female weight (grams)	W	18.8	0.132	0.0193
Sex ratio by weight (females/total)	R	0.472	4.90×10^{-4}	0.0469
Batch fecundity (eggs per batch per mature female)	F	10845	171730	0.0382
Fraction of mature females spawning per day	S	0.120	9.47×10^{-5}	0.0813
Spawning biomass (MT)	B_e	378,000	945×10^9	0.257

The sex ratio for each trawl is determined from the first 50 fish. Average weights by sex per trawl are estimated from the first 5 males and the first 20 females, where the weight of hydrated females is adjusted using equation (8). The trawl average, $\bar{R}_i$, is the estimated total weight of the females in the first 50 fish subsampled, divided by the estimated total weight of the first 50 fish. The m_i in equations (6) and (7) for this parameter is the estimated total weight of the first 50 fish. For both sexes, both mature and immature fish are included because of the difficulty of distinguishing between mature and immature males. The estimate for sex ratio is 0.472 (equation [6]), and its estimated variance (equation [7]) and coefficient of variation are 4.90×10^{-4} and 4.69%, respectively.

Biomass Estimate and Variance

The parameter estimates and their variances given above are summarized in Table 1. The resultant estimate of anchovy spawning biomass using equation (1) is 378,000 MT (417,000 short tons). The approximate variance is calculated according to equation (2), where covariance terms are included only for those pairs of variables with sample correlations that are significantly different from zero. The sample correlations between P_o and the adult parameters are assumed to be zero because they are derived from two different surveys (the plankton survey and the trawl survey) and thus cannot be estimated. Of the adult parameters, only cov(W,F), cov(R,W), and cov(F,R) are significant, with values of 110, 0.00271, and 1.57, respectively. The approximate variance of the biomass estimate is 9.45×10^9, and standard error is 97,200 MT, for a coefficient of variation of 25.7%. The approximate 95% confidence interval is ± 194,000 MT.

EQUIVALENT LARVAL CENSUS ESTIMATE OF BIOMASS

The anchovy management plan presently requires that the annual harvest quota for the U.S. fishery be based on an annual estimate of spawning biomass (Smith 1972; Huppert et al. 1980). The PFMC has interpreted the plan to require an equivalent larval census biomass estimate. The 1982 survey was designed to generate an estimate of the biomass based on the egg production and fecundity of the population, but was not designed to directly generate a larval census estimate of biomass.

It is possible to generate an equivalent larval census estimate of biomass by estimating the number of larvae resulting from the measured production of eggs (Stauffer 1983). To do so, the mortality rates of both eggs and larvae are required. The abundance of larvae can then be extrapolated to an annual census using historical proportions of quarterly abundances. The spawning biomass is assumed to be proportional to the annual census; the constant of proportionality was determined from a regression of adult sardine biomass on the annual census of sardine larvae, and an assumption of sardine to anchovy annual fecundity of 1:2 (Smith 1972).

During the 1982 egg production cruise, 96 plankton samples were obtained using the bongo net at standard CalCOFI stations (Figure 10). Anchovy larvae were found at 69 of the stations. In the following sections we discuss: (1) the production curve of the larvae derived from the size-specific catch curve; (2) an equivalent annual larval census derived from the population production of eggs and the subsequent mortality of both eggs and larvae; and (3) the discrepancy between the egg production estimate of biomass and the equivalent larval census estimate.

Production Curve

The larvae were grouped into 12 size categories (yolk-sac to 15 mm), and catches were adjusted for variations in the volume of water filtered per m of depth. Bias corrections were also applied for extrusion of small larvae through the meshes of the net and avoidance of the net by large larvae. The adjusted catches were divided by the duration of growth, through each size class, to estimate the age-specific production of larvae (P_t). The adjustments were accomplished by fitting a weighted negative binomial model to the sample frequency distributions of each size class. Each observation is weighted by a factor that is the product of the various adjustments, and the means of the final distributions are unbiased estimates of production (P_t). The procedure was developed in a series of papers: Bissel 1972; Zweifel and Smith 1981; Hewitt 1981, 1982; Hewitt and Methot 1982; Hewitt and Brewer 1983. The calculations are summarized in Table 2, and the results are described in Figure 11.

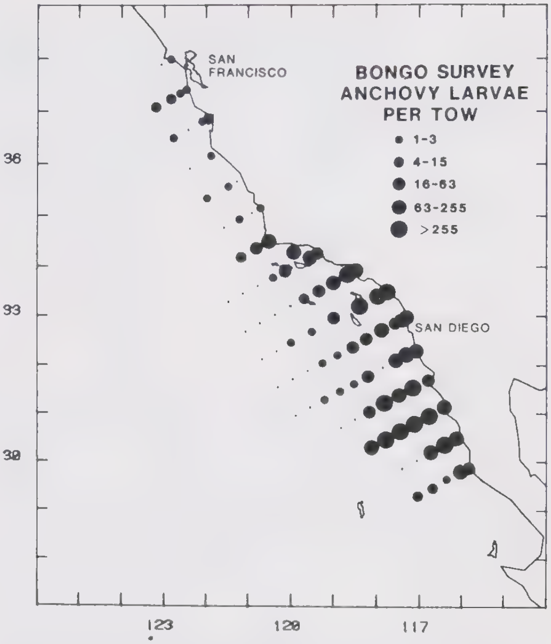

Figure 10. Geographic distribution of anchovy larvae as determined from standard CalCOFI ichthyoplankton bongo tows taken at 96 stations during the 1982 egg production survey.

It is clear, from a log-transform plot, that a constant mortality model, $dp/dt = -cP$ will not adequately describe the data. A variable mortality model may be devised by defining c as a function of age.[6] Several forms would adequately describe the data, but for reasons of mathematical tractability we may use:

$$\frac{dP}{dt} = -\frac{\beta}{t}P . \tag{11}$$

As t increases, the instantaneous rate of change of production decreases (improving survival with age). The above expression may be rearranged, integrated, and the integration constant determined at the age of hatching (t_h):

$$P_t = P_h\left(\frac{t}{t_h}\right)^{-\beta} \text{ for } t \geqslant t_h. \tag{12}$$

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[6] Variable mortality rate may be defined as a function of age, size, or population abundance. The important point is that the number of deaths is modeled as a portion of those living. N. Lo, SWFC, suggested the form used here.

TABLE 2
Size-Specific Catches of Anchovy Larvae and Age-Specific Estimates of Daily Production

Preserved size (mm)	Fraction retained by net[1]	Average adjustment for sampling and sorting variability[2]	Average duration of growth[3] (days)	Average catch $\left(\frac{\text{larvae}}{\text{tow}}\right)$	P_t[4] $\left(\frac{\text{larvae}}{\text{m}^2\text{-day}}\right)$	Age[3] since fertilization (days)
2.50	0.21	1.91	3.59	29.99	20.82	4.42
3.75	0.51	1.99	3.51	26.91	7.56	8.00
4.75	0.69	1.98	2.58	16.91	4.80	11.07
5.75	0.73	2.18	2.38	12.12	3.20	13.62
6.75	0.73	2.18	2.24	8.93	2.51	15.74
7.75	0.68	2.20	2.16	6.75	2.09	18.13
8.75	0.61	2.22	2.12	5.10	1.78	20.24
9.75	0.60	2.09	2.11	3.38	1.28	22.67
10.75	0.54	2.86	2.12	1.70	0.52	24.92
11.75	0.56	2.27	2.14	1.06	0.39	27.01
12.75	0.46	1.75	2.19	0.51	0.29	28.88
13.75	0.57	2.11	2.29	0.33	0.12	31.93

[1] Extrusion corrections are based on relative retention rates between 75-micrometer and 505-micrometer mesh nets (Lo, SWFC pers. comm.) Avoidance corrections are based on night and day catch comparisons using bongo data from 1978 and 1979 (Hewitt and Methot 1982). Fraction of larvae retained in the net is estimated as Σ col. 5/Σ (col. 5/col. 2); $r = 0.4$.
[2] Accounts for partial sorting of samples and standardizes sampling volume to 1 m^2 per m of depth.
[3] Temperature-dependent embryonic growth is determined from laboratory experiment (Lo, SWFC pes. comm.), and post-yolk-sac growth follows Methot's (1981) description.
[4] Production rates (P_t) may be estimated by dividing the average catch by the product of columns 2, 3, and 4. In practice, however, P_t is the mean of a weighted negative binomial model fit to the distribution of individual observations (ie., plankton tows).

This expression defines the larval production curve. The average standing stock of larvae is the area under the curve, and it may be determined by integrating the above expression between t_h and 30 days (the maximum age effectively caught with a standard plankton tow). Thus:

$$N = A \int_{t_h}^{30} P_h \left(\frac{t}{t_h}\right)^{-\beta} dt$$

$$= A \frac{P_h t_h}{\beta - 1} \left(1 - \left(\frac{t_h}{30}\right)^{\beta - 1}\right) \qquad (13)$$

where N is the average standing stock of larvae and A is the area of the survey.

Equivalent Annual Larval Census

An equivalent larval census estimate of biomass may be derived by reducing the production of eggs to the production of hatching larvae via egg mortality and then integrating the larval production curve over age to estimate average standing stock of larvae. The average standing stock is converted to the annual larval census by a factor[7] of 2.12. The standard sampler would retain a fraction (r) of these larvae; the remainder are extruded through the meshes, and a small portion avoid capture. Finally, the annual larval census is converted to spawning biomass using the historical conversion factor of 8.9×10^{-8} MT/larva. Thus:

$$\hat{B}_l = N(2.12)\, r(8.9 \times 10^{-8}) \qquad (14)$$

where: r = fraction of larvae retained in standard sampler,

$$P_h A = P_0 A s$$

$$N = P_0 A s \left(\frac{t_h}{\beta - 1}\right)\left(1 - \left(\frac{t_h}{30}\right)^{\beta - 1}\right)$$

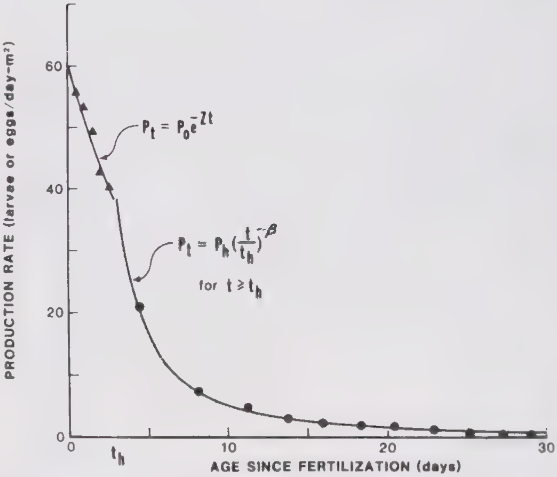

Figure 11. Changes in the production rate of eggs and larvae with time since fertilization. Production of eggs (triangles) was estimated from the CalVET sample, and the production of larvae (dots) was estimated from the CalCOFI bongo sample. The shaded area under the larval production curve is the average standing stock of larvae *(N)*.

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[7] The annual larval census is the sum of the average standing stock in each quarter. Stauffer and Picquelle (1980) describe the historical proportions of the quarterly values as 1:1/.06/.06, so that the annual larval census is equal to 2.12 times the average standing stock over the first 2 quarters.

TABLE 3
Projected and Observed Larval Census Estimates of Spawning Biomass and Related Parameters

	1980	1981		1982
		Feb.	Apr.	
Population production P_oA of eggs (eggs/day)	23.97×10^{12}	19.07×10^{12}	11.46×10^{12}	12.30×10^{12}
Egg mortality rate z	0.453	0.138	0	0.158
Time to hatch (days) t_h	2.71	2.75	2.75	2.91
Survival to hatch $s = e^{-zt}h$	0.293	0.684	1.000	0.631
Coefficient in larval mortality β model	1.7999	1.7058	1.7058	1.7085
Retention r	0.4	0.4	0.4	0.4
Projected larval census B_l estimate of spawning biomass (MT)	1.533×10^6	3.126×10^6	2.746×10^6	1.866×10^6
Larval census estimate of B_l spawning biomass (MT)	1.611×10^6	2.544×10^6	2.544×10^6	—
Daily fecundity $\left(\frac{\text{eggs/day}}{\text{ton}}\right) q$	30.28×10^6	33.03×10^6	33.84×10^6	32.53×10^6

and P_hA is the population production of hatching larvae, P_oA is the population production of eggs, s is the fraction of egg production surviving to hatch, and $\hat{B}_l$ is the equivalent larval census estimate of spawning biomass (MT).

When equation (14) was applied to 1980 and 1981 surveys, which generated both egg production and larval census estimates, the larval census was similar to that estimated from the production of eggs (average ratio = 1.09; range 0.95 to 1.23; Table 3). By rewriting equation (1) as:

$$B_e = \frac{P_oA}{q}$$

where B_e is the egg production estimate of spawning biomass, P_oA is the daily population production of eggs, and q is the daily fecundity on a weight basis $= RFS/kW$, we may relate the equivalent larval census estimate of biomass ($\hat{B}_l$) to the egg production estimate of biomass (B_e) using equation (14):

$$\hat{B}_l = B_e\, qs$$

$$\left(\frac{t_h}{\beta - 1}\right)\left(1 - \left(\frac{t_h}{30}\right)^{\beta - 1}\right) r\,(18.9 \times 10^{-8}). \quad (15)$$

Thus the equivalent larval census estimate of spawning biomass may be calculated from the egg production estimate of biomass by adjusting the latter for fecundity, egg survival, larval survival, and larval retention in the standard ichthyoplankton sampler historically used for larval census estimates. Because the larval census estimate of biomass assumes a fixed fecundity, $\hat{B}_l$ may be calculated from the population production of eggs, without consideration of the adult reproductive parameters, using equation (14).

Equation (14) was applied to the data presented in this report; the parameter values are listed in Table 3. The 1982 equivalent larval census estimate of spawning biomass is 1.866×10^6 MT (2.060×10^6 short tons); the equivalent annual larval census is $20{,}966 \times 10^9$ larvae.

Discrepancy between the Biomass Estimates

The equivalent larval census estimate of spawning biomass (1.866×10^6) is nearly five times the egg production estimate of spawning biomass (0.378×10^6 MT). One or more of three factors may be the cause of this discrepancy: (1) sampling errors between the ichthyoplankton gears; (2) variability in the conversion factor relating the larval census to the spawning biomass (resulting from variability in the population fecundity and survival of young, which are assumed to be constant in the larval census method); and (3) systematic inaccuracy in the conversion factor relating anchovy larvae to anchovy spawners.

The projected abundance of larvae and the measured abundance of larvae agree reasonably well for three surveys (Table 3). This indicates that the two sampling gears (CalVET net, used to sample eggs, and the CalCOFI bongo net, used to sample larvae) yield consistent and compatible estimates of ichthyoplankton production. It is possible to predict the catch of one gear from the catch of the other. The discrepancy between the biomass estimates is thus not due to inaccuracy or imprecision in the ichthyoplankton sampling.

The population fecundity and survival of larvae did not vary considerably among the three surveys (Table 3). Egg survival, however, did vary, ranging from an estimated 29% survival in 1980 to 100%

TABLE 4
Adjustment of Larval Census Estimates of Spawning Biomass for Variability in Egg Survival

Year	1980	1981		1982
		Feb.	Apr.	
S	0.293	0.684	1.000	0.631
B_e	792×10^3	577×10^3	339×10^3	378×10^3
B_l	1611×10^3	2544×10^3	2544×10^3	1866×10^3
$\frac{0.650}{S}$	2.218	0.950	0.650	1.030
Adj. B_l	3573×10^3	2417×10^3	1654×10^3	1922×10^3
$\frac{\text{Adj. } B_l}{B_e}$	4.5	4.2	4.9	5.1
$\frac{0.300}{S}$	0.977	0.439	0.300	0.475
Adj. B_l	1574×10^3	1117×10^3	763×10^3	886×10^3
$\frac{\text{Adj. } B_l}{B_e}$	2.0	1.9	2.3	2.3
$\frac{1.000}{S}$	3.412	1.462	1.000	1.585
Adj. B_l	5498×10^3	3719×10^3	2544×10^3	2957×10^3
$\frac{\text{Adj. } B_l}{B_e}$	6.9	6.4	7.5	7.8

survival in April 1981. Low egg survival implies that a low larva-to-spawner ratio actually existed and that spawner biomass was underestimated relative to surveys where egg survival was high. To investigate this effect, we assumed that an egg survival rate of 65% prevailed during all the surveys, and we proportionally adjusted the larval census estimates of spawning biomass (Table 4). The adjusted larval census estimates of spawning biomass are consistently 4 to 5 times greater than the egg production estimates of spawning biomass, indicating a systematic bias. If we assume an egg survival of 30%, the ratio decreases to 2; whereas an egg survival of 100% implies that the larval census overestimates spawning biomass by a factor of 7 (Table 4). Thus by considering variability in egg survival we have shown that the discrepancy between the two biomass estimates can be reconciled by a single factor for all the surveys.

Finally, we consider the conversion factor relating the annual census of anchovy larvae to anchovy spawners. This factor was determined for the sardine by regressing virtual population estimates of the adult stock on the annual sum of quarterly larval census estimates (Smith 1972). The proportionality was extended to the anchovy by estimating the relative annual fecundity (anchovy: sardine) to be 2 (Smith 1972); i.e., each anchovy larva represented only half the weight of adult fish that a sardine larva did. We demonstrated above that the larval census estimate of biomass (when adjusted for variations in egg survival) exceeds the egg production estimate of biomass by a fixed factor. We suggest that this bias results from inaccuracy in the anchovy/sardine relative annual fecundity (on a weight basis). The average of the four observations of egg survival is our best estimate of the long-term average egg survival (65%); use of this value implies that the relative fecundity is approximately 4.5 times the previously accepted value. We suggest that the anchovy spawns approximately 9 times as many eggs per gram throughout the year as does the sardine. This may be explained by increasing the batch fecundity per gram and shortening the interval between spawnings (these relationships between the reproductive parameters of anchovies and sardines have been observed in Peru by P. Smith [pers. comm.]).

Thus the discrepancy between the larval census estimates and the egg production estimates of spawning biomass can be explained by variation in egg survival and inaccuracy in estimating the average proportionality between the larval census and the spawning biomass. We further consider the egg production method to be more precise (because it considers the rate at which eggs die) and more accurate (because of the underestimate of anchovy fecundity) than the larval census method.

ACKNOWLEDGMENTS

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ANALYZING THE WIDTH OF DAILY OTOLITH INCREMENTS TO AGE THE HAWAIIAN SNAPPER, *PRISTIPOMOIDES FILAMENTOSUS*

Stephen Ralston[1] and Garret T. Miyamoto[2]

ABSTRACT

Studies of otolith microstructure in Hawaiian snapper, *Pristipomoides filamentosus*, indicate that growth increments are deposited daily in immature fish (<40 cm FL and <3 yr of age). Laboratory experiments with tetracycline-injected fish and analysis of modal progression in size-frequency distributions of field-sampled fish validate this conclusion. Given a 1:1 correspondence between increments and days, one can determine otolith growth rate by measuring increment width. Based on the relationship between otolith growth rate and otolith length, we conclude that increment deposition in mature *P. filamentosus* is episodic, i.e., interrupted.

Using regression analysis, a model is developed relating otolith growth rate to otolith length. It is shown that integration of the regression equation provides estimates of the age of individual fish. Assumptions involved in the model are discussed, and it is concluded that this method of aging adequately represents the growth of *P. filamentosus* when time is measured on a scale of years. Age estimates derived here are entirely consistent with those of related forms (Lutjanidae) reported in the literature.

Studies of fish otoliths have now revealed that these calcified structures often grow by daily accretion of increments, in a manner analogous to the annual rings of trees. Pannella (1971, 1974) was the first to demonstrate this, and now many other researchers have substantiated and extended his findings to a wide variety of temperate and tropical species in both marine and freshwater environments (Brothers et al. 1976; Struhsaker and Uchiyama 1976; Le Guen 1976; Ralston 1976; Timola 1977; Taubert and Coble 1977; Barkman 1978; Brothers 1978; Methot and Kramer 1979; Dunkelberger et al. 1980; Pannella 1980; Schmidt and Fabrizio 1980; Steffensen 1980; Wild and Foreman 1980; Wilson and Larkin 1980; Worthmann 1980; Brothers and McFarland 1981; Mugiya et al. 1981; Uchiyama and Struhsaker 1981; Tanaka et al. 1981; Ralston and Miyamoto 1981; Campana and Neilson 1982; Watabe et al. 1982; Radtke and Dean 1982; Radtke[3]). Daily growth structures from a wide variety of plant and animal tissues were known for some time prior to Pannella's discovery (Choe 1963; Neville 1967). In fact, several publications which predate his work presented photographs of otoliths in which typical daily increments are evident (Hickling 1931; Morris and Kittleman 1967; Degens et al. 1969), yet their temporal significance was unappreciated at the time.

We are now developing a more sophisticated understanding of the processes which control the incremental growth of otoliths, with multiple factors influencing accretion, including photoperiod, food, and temperature (Hickling 1931; Irie 1960; Degens et al. 1969; Mugiya 1974, 1977; Taubert and Coble 1977; Brothers 1978; Dunkelberger et al. 1980; Pannella 1980; Mugiya et al. 1981; Tanaka et al. 1981; Watabe et al. 1982; but see Campana and Neilson 1982). Furthermore, some studies have revealed the existence of subdaily increments (Taubert and Coble 1977; Brothers 1978; Pannella 1980; Wilson and Larkin 1980; Campana and Neilson 1982) which complicates considerably the temporal interpretation of increment periodicities.

A powerful application of daily increment research has been the use of increment width as a measure of otolith and somatic growth rate. Pannella (1974) first presented this view when he stated, "Increment thickness is the spatial expression of time" and " . . . is the faithful expression of the conditions and rate of growth." In substantiating this claim, Struhsaker and Uchiyama (1976), Taubert and Coble (1977), and Barkman (1978) showed that otolith ring counts depend purely on specimen age and not otolith size. Slow-growing fish had small otoliths, while in comparably aged fast-growing fish the otoliths were larger but contained no more increments. Moreover, Wild and Foreman (1980) used the change in otolith dimension subsequent to mark-

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[1] Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.

[2] Department of Animal Science, University of Hawaii, Honolulu, HI 96822.

[3] Radtke, R. L. Scanning electron microscope observations of daily increments and structure in otoliths of the adult tropical fish *Pristipomoides filamentosus*. Manuscr. in prep. Pacific Gamefish Foundation, P.O. Box 25115, Honolulu, HI 96825.

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ing to estimate change in fish length and, ultimately, somatic growth rate. Similarly, Brothers et al. (1976) and Methot and Kramer (1979) numerically integrated increment thickness data to estimate age. Although of some significance, no formal or detailed treatment of the subject was presented. More recently Methot (1981) has measured the widths of the outer three daily increments in the otoliths of larval fishes, using them as explicit measures of recent daily growth rate. Brothers (1981) discussed this kind of application and cautions against short-term uncouplings of otolith growth with changes in fish length.

In this paper, we intend to analytically formalize the concept that increment width can be used as a measure of otolith growth rate. This eliminates the constraint of having to count all increments in an otolith, providing a framework for studying age and growth in large, slow-growing species of fish in which increment microstructure frequently becomes ambiguous with age (Brothers 1979; Pannella 1980). Rather than attempting a numerical solution to this problem, we have analytically integrated increment growth-rate data obtained from the otoliths of Hawaiian snapper, or opakapaka, *Pristipomoides filamentosus* (Lutjanidae). This is a commercially important species of bottomfish harvested in the Hawaiian deep-sea handline fishery (Ralston 1981; Ralston and Polovina 1982). While admittedly sacrificing some of the extreme precision theoretically possible with daily increments, the intent here is to provide reasonably reliable age estimates, economically obtained, when age is measured on a scale of years. Preliminary results of this research have been reported elsewhere (Ralston and Miyamoto 1981).

METHODS

Marking Experiment

A marking experiment was done to validate the existence of daily growth increments in opakapaka. Otoliths are composed primarily of the aragonitic crystalline form of calcium carbonate in association with small amounts of otolin protein (Hickling 1931; Irie 1960; Degens et al. 1969). The presence of calcium carbonate allows otoliths to be successfully marked in vivo with the antibiotic tetracycline (Blacker 1974; Wild and Foreman 1980; Campana and Neilson 1982). A dated, visible time-mark in otoliths provides direct validation of the periodicity of presumed daily increments.

Six juvenile opakapaka (30-34 cm FL (fork length)), captured by hook and line, were acclimated to a 1,135 l flowthrough aquarium. The fish were exposed to a natural photoperiod through an overhead skylight and were fed to satiation twice daily (midmorning and late afternoon). All six fish were initially in good condition, and after 12 d they appeared well adjusted to the tank, having resumed what seemed to be normal feeding behavior.

Three 1 kg specimens were injected intraperitoneally with 30 mg of oxytetracycline (dosage from A. Wild[4]). Following injection, all six fish were exposed for 18 h to 125 ppm acetazolamide in seawater (dosage from J. Dean[5]). This compound has been shown to affect otolith calcification by inhibition of carbonic anhydrase (Mugiya 1977), providing a simple means of creating a checkmark on otoliths. The fish resumed feeding 2 d after treatment. One fish jumped out of the tank 27 d later, and the experiment ended prematurely when the remaining five specimens died unaccountably 38-39 d after treatment.

Preparation of Otoliths

All otoliths in this study were prepared for viewing as outlined in Ralston and Miyamoto (1981). Thin sections (0.5 mm) were made through the focus along a frontal plane to the most distal portion of the postrostrum (Figs. 1, 2). Preliminary observations showed that increment counts made in a transverse plane were less than those made from frontal sections, presumably due to pinching and coalescing of rings along the shorter transverse axis (Pannella 1974; Taubert and Coble 1977; Dunkelberger et al. 1980). Tetracycline marks were obliterated by the clearing agent (Euparal[6]) and were located prior to etching by viewing with an ultraviolet fluorescence microscope. In addition, several otoliths were prepared for scanning electron microscope (SEM) examination.

Otolith Growth Rate and Specimen Age

After otoliths had cleared, they were read with a compound binocular microscope using transmitted light at a magnification of 400×. The distance in microns (μm) between the focus and the postrostral margin, representing the total length (L) of the otolith along the postrostral radius, was measured with a

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[4] A. Wild, Inter-American Tropical Tuna Commission, La Jolla, CA 92037, pers. commun. May 1980.

[5] J. Dean, Professor, Belle Baruch Institute, University of South Carolina, Columbia, SC 29208, pers. commun. May 1980.

[6] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

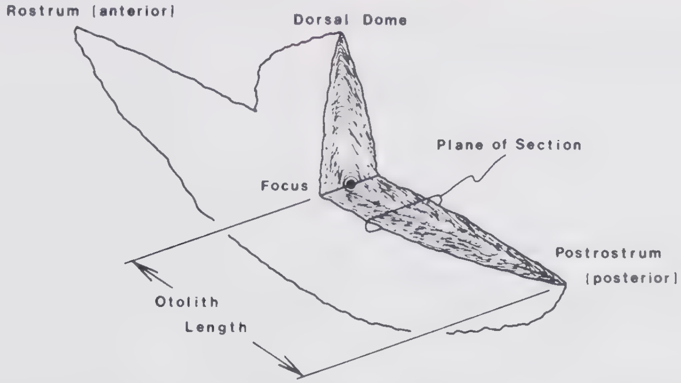

FIGURE 1.—Schematic of an otolith from *Pristipomoides filamentosus* with specific points of reference discussed in the text.

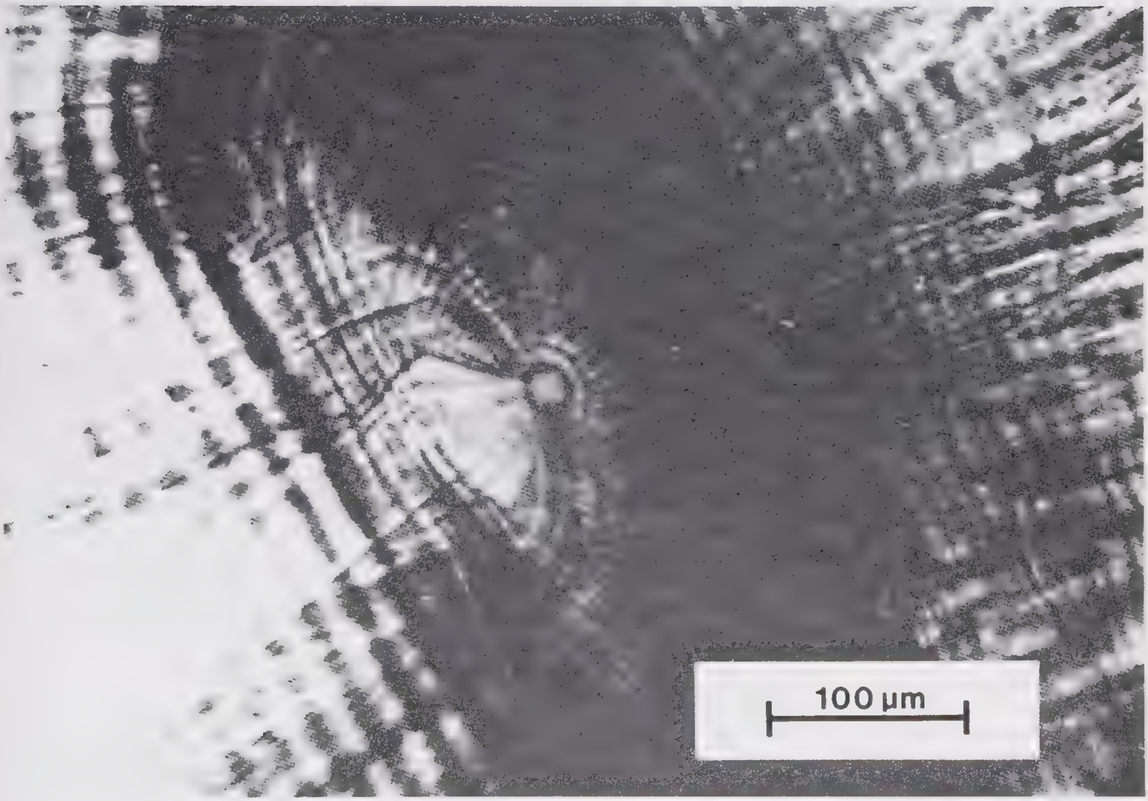

FIGURE 2.—Photomicrograph through the nuclear core region of an otolith from *Pristipomoides filamentosus*. Note increments become compressed in this area.

calibrated ocular micrometer (Fig. 1). Readings were then made at selected points along the postrostral growth axis, wherever increment microstructure was clearly viewed. At such locations the average width of increments was determined by counting the number of increments visible ($\bar{x} = 15.95$, SD $= 11.24$) and by measuring the radial length of the short segment in which the increments were observed. In addition, the distance between the midpoint of the sample region and the otolith focus (ℓ) was measured along the same postrostral growth axis. As many readings as possible were made from each preparation ($\bar{x} = 31.9$), subject to the constraint that counts be made only in regions where increments were clear.

Data were summarized for each specimen by computing the ratios of segment length in μm to the number of increments included at each specific segment examined in the preparation. These figures represent the average increment width at given points in the otolith. Under the assumption that one increment forms each day, it is possible to approximate the otolith growth rate on a size-specific basis as follows:

$$\frac{\Delta \ell}{\Delta \text{ increments}} = \frac{\Delta \ell}{\Delta t} \simeq \frac{d\ell}{dt}$$

where $\Delta \ell$ is the change in length (μm) of the otolith over a given subregion, and Δt is the change in time (days). The finite approximation to the differential was always computed on a sufficiently small scale of time and length.

Given the series of ordered pairs, $\frac{d\ell}{dt}$ at otolith length ℓ, it is possible to evaluate the functional relationship between these quantities, $\frac{d\ell}{dt} = f(\ell)$, and to estimate the parameters of the function using regression analysis. The regression equation can then be solved by separation of variables and treated as a definite integral, bounded by the focus and the total length (L) of the otolith at death, providing an explicit estimate of age in days (T). That is:

$$\int_{t=0}^{T} dt = \int_{\ell=0}^{L} [f(\ell)]^{-1} d\ell. \qquad (1)$$

Size at Maturity

Samples of opakapaka gonads were obtained from throughout the Hawaiian Archipelago. Sampling was haphazard with respect to both time and location. Gonads were preserved in 10% Formalin until examined, when they were weighed to the nearest gram after excess moisture had been removed by blotting with a paper towel. Sex was determined by microscopic examination of smeared gonadal tissues, and ovaries were staged according to the following classification:

Stage I. Inactive ovary
  a) egg diameters 75-100 μm
  b) transparent primary oocytes in ovary
  c) nucleii faintly visible
  d) eggs ovoid
Stage II. Developing ovary
  a) egg diameters 100-325 μm
  b) some opaque eggs in ovary
  c) nucleii clearly visible
  d) eggs wedge-shaped
Stage III. Gravid/spawning ovary
  a) egg diameters 325-850 μm
  b) presence of oil globules
  c) evidence of yolk granules
  d) eggs ovoid

RESULTS

Typical looking increments are found in the sagittae of opakapaka (Fig. 3). In this SEM photograph the distinct incremental growth of the otolith is readily apparent, with a structure similar to that described in previous descriptions of daily increments. Discernible under high magnification is a more deeply etched, discontinuous zone which transects the radial growth of aragonite crystals found in the incremental zone (Hickling 1931; Pannella 1971, 1974, 1980; Blacker 1975; Brothers et al. 1976; Timola 1977; Dunkelberger et al. 1980; Mugiya et al. 1981; Tanaka et al. 1981; Watabe et al. 1982; Radtke footnote 3).

Tetracycline Validation

Photomicrographs of a sagittal section through the otolith of one of the three experimental fish injected with oxytetracycline are presented in Figure 4. In the upper photograph the specimen was illuminated with ultraviolet light, clearly showing the fluorescing tetracycline checkmark. The lower photograph shows the same specimen illuminated with visible light. A discontinuity coincident with the tetracycline label is evident. We interpret this latter checkmark to be due to exposure to acetazolamide and handling trauma. The close coincidence of the two marks allowed us to positively identify the experimentally induced checkmark in all six specimens.

The results of marginal increment counts from these fish are summarized in Table 1. Several sections were taken from each otolith, although not all preparations were readable. Furthermore, because the quality of all sections was poor, multiple counts of each section were made. The figures under the heading "Number of marginal increments" represent the range of counts.

It is evident from these data that the number of increments deposited on the otoliths after marking was quite similar to the number of days elapsed after the fish were marked. Since these fish were stressed dur-

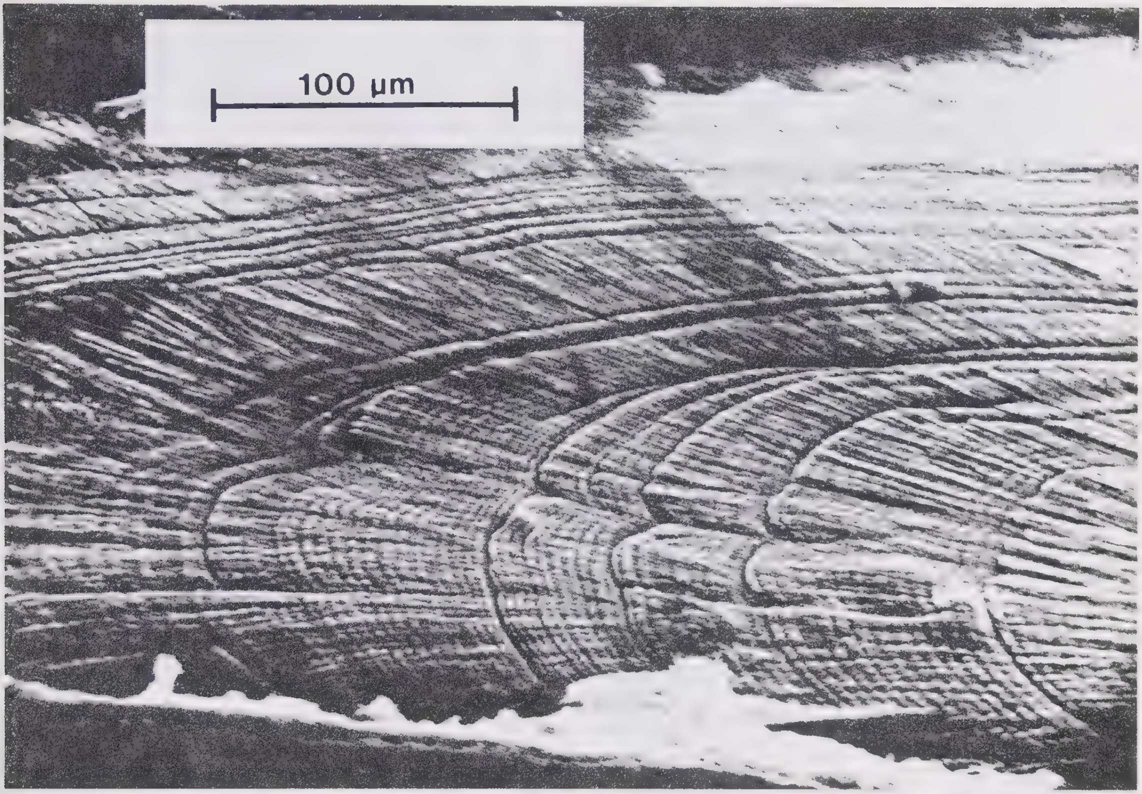

FIGURE 3.—A scanning electron microscope (SEM) photograph of a sagitta from *Pristipomoides filamentosus*, showing radial development of aragonite crystals transected by incremental and discontinuous zones.

ing captivity and did not feed for 2 d after treatment, we interpret these as confirming results. During the course of the experiment a 1:1 correspondence was maintained between increments and days, demonstrating the presence of daily marks rather than features entrained to other periodicities (e.g., subdaily marks).

Otolith Growth

Due to the likelihood of allometric relationships, it is important to distinguish between the growth of the otolith and the growth of the whole fish. Figure 5 shows that the slope of the log-linear power function regression of otolith length on fork length, based on measurements from 66 individuals, is significantly <1 ($\beta = 0.6286$, $t = -14.12$, df $= 64$). This is typical of many fish species (Hickling 1933; Templeman and Squires 1956; Blacker 1974; but see Taubert and Coble 1977) and implies that the growth rate of opakapaka otoliths $\left(\frac{d\ell}{dt}\right)$ is not related in a simple linear fashion to somatic growth rate.

TABLE 1.—The results of marginal increment counts on tetracycline- and acetazolamide-marked otoliths of *Pristipomoides filamentosus*.

Specimen no.	Days marked	Number of marginal increments
E-1, Section D	27	24-27
E-2, Section B	38	33-39
Section C		35-38
E-3, Section F	38	30-31
E-4, Section A	38	30-32
Section B		30-38
E-5, Section A	38	37-39
Section C		30
E-6, Section C	39	27-30
Section D		35-39

A total of 81 sagittae from 68 individuals were examined with light microscopy for presence of daily increments. In 13 cases both left and right otoliths from the same individual were viewed. These 81 samples provided 2,957 separate estimates of otolith growth rate along the postrostral growth axis. Initially the data were pooled to elucidate the functional relationship between otolith growth rate and otolith length. The results are presented in Figure 6.

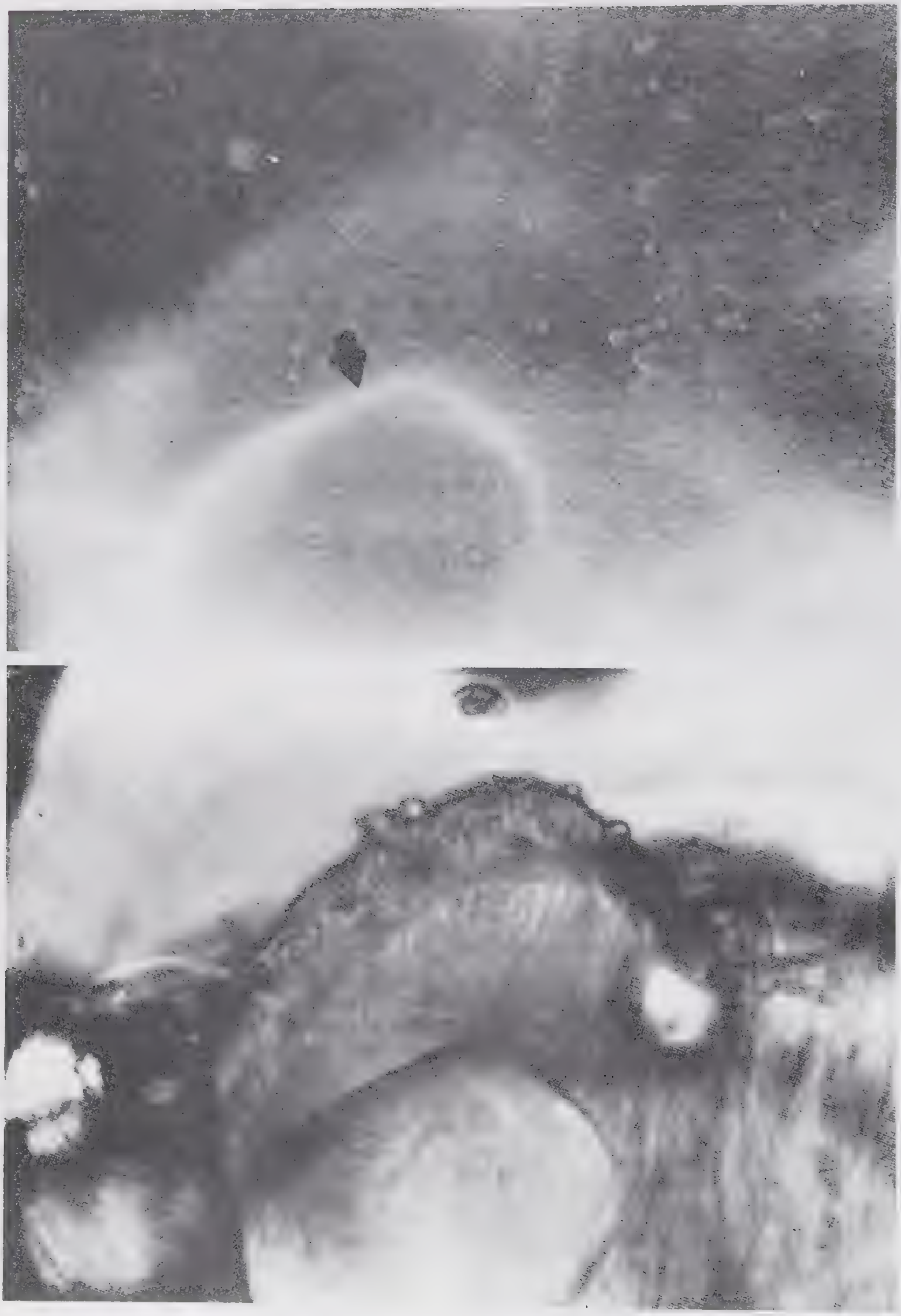

FIGURE 4.—(top) Photomicrograph of a tetracycline-marked otolith of *Pristipomoides filamentosus*, illuminated by ultraviolet light. Note checkmark at arrow. (bottom) Photomicrograph of the same sample illuminated under visible light. 300× magnification.

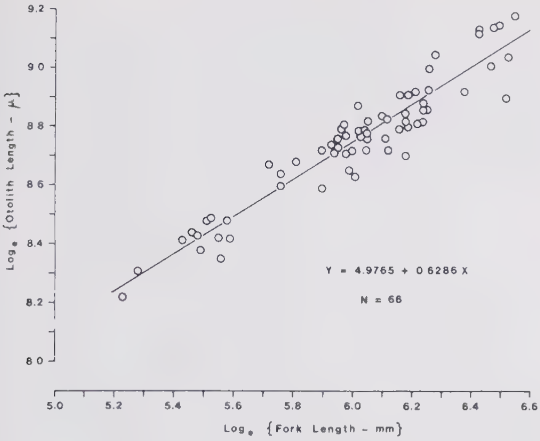

FIGURE 5.—Relationship between otolith length and fork length in *Pristipomoides filamentosus*.

There is pronounced curvilinearity in the data, as well as heteroscedastic variance. The von Bertalanffy growth model (Ricker 1979) asserts that somatic growth rate in length is a linear decreasing function of length, with the X-intercept defining the asymptotic upper bound on growth (L_∞). The observation that the growth-rate curve of opakapaka otoliths is a concave (upwards), monotonic decreasing function of otolith length (Fig. 6) is consistent with this notion, given the previously deduced allometric relationship between fork length and otolith length.

Growth-rate data were logarithmically transformed to linearize the trend line and stabilize the variance (Fig. 7). It is evident that once the otolith reaches about 6,000 µm in length, an alteration occurs in the rate (slope) at which log-transformed growth rate declines, maintaining a higher rate than would be expected otherwise. This noticeable change in slope is apparently due to attainment of reproductive maturity.

Of those female opakapaka collected during the summer spawning season (Kikkawa 1980; Ralston 1981), the incidence of gravid/spawning ovaries is strongly dependent upon fish size (Fig. 8). These data indicate that female opakapaka reach reproductive maturity at about 40 cm FL. Fish this length have otoliths about 6,250 µm long (Fig. 5). Thus the distinct change in trend of otolith growth rate coincides closely with maturation. Males show a similar pattern of gonad maturation (Ralston 1981).

Based on these observations, it is likely that periods of episodic growth commence in opakapaka otoliths with the onset of maturity. That growth dynamics should improve at this time, as suggested by a moderation in the decline of log-transformed otolith

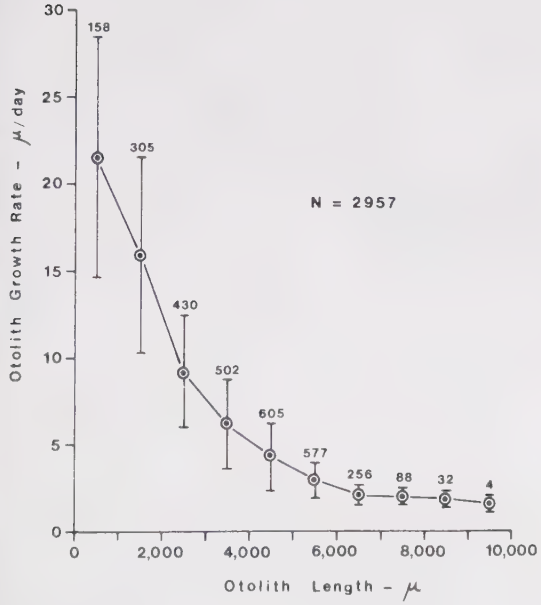

FIGURE 6.—Relationship between otolith growth rate (increment width) and otolith size in *Pristipomoides filamentosus*. Points represent means bracketed by standard deviations. Sample sizes are given above each length class.

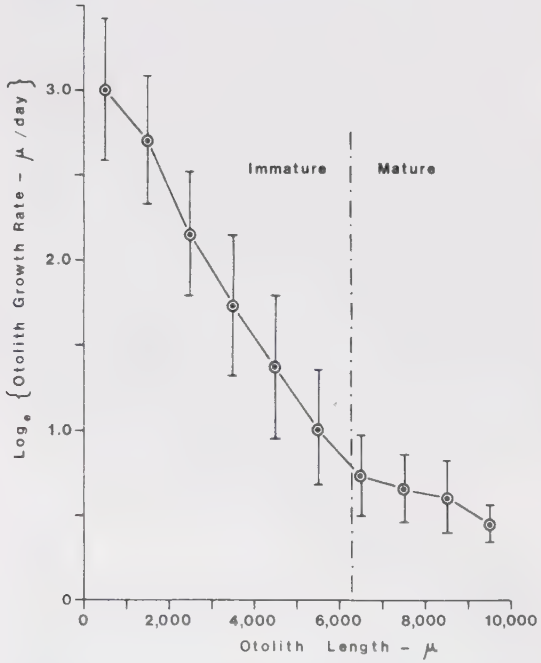

FIGURE 7.—Linearization of otolith growth rate data by logarithmic transformation for *Pristipomoides filamentosus*. Points represent means bracketed by standard deviations.

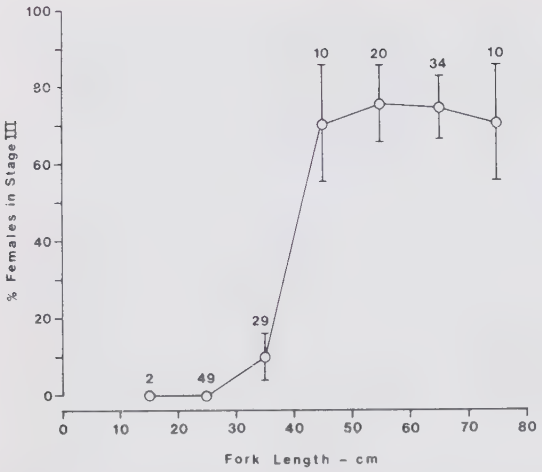

FIGURE 8.—Maturation in *Pristipomoides filamentosus* female. Stage III represents gravid/spawning individuals. Only samples collected during the spawning season are presented. Points represent means bracketed by standard deviations. Sample sizes are given above each length class.

growth rate, is completely counterintuitive to our understanding of the trade offs involved in optimizing growth and reproductive processes. Rather, it is more likely that episodic growth leaves an incomplete time record in the otolith (i.e., increments are not deposited) while concurrently, changes in otolith length are tightly coupled to changes in fork length (see Figure 5 where $r^2 = 0.899$). The resulting process would tend to underestimate Δt and thus to overestimate $\frac{d\ell}{dt}$. This hypothesis of interrupted otolith growth could explain the anomalous trend in otolith growth rates; consequently, we have regarded all data from otolith lengths $>6{,}000$ μm to be equivocal. We excluded these points from the remaining analyses, reducing the data set by 13% (2,957 ordered pairs to 2,577).

It is evident from Figure 7 that for otoliths $\leq 6{,}000$ μm the logarithmic transformation was effective in linearizing the trend line and in stabilizing the variance, allowing the formulation of an analytical model describing the functional relationship between $\frac{d\ell}{dt}$ and ℓ. We write

$$\log_e \left(\frac{d\ell}{dt}\right) = \alpha - \beta\ell + \varepsilon \qquad (2)$$

where ℓ is otolith length in μm, t is time in days, α and β are model parameters, and ε is a normal random variable with mean zero and finite variance. When this model is cast in the form of Equation (1) and integrated, the solution is

$$\hat{T} = (e^{\alpha}\beta)^{-1}\,(e^{\beta L} - 1) \qquad (3)$$

where T is the estimate of age in days, and L is the total length of the otolith along the postrostral radial axis. Thus, to estimate the age of a sample specimen, one need only acquire estimates of α, β, and L.

Von Bertalanffy Growth Curve

A regression of log-transformed otolith growth rate against otolith length (Equation (2)) was performed for each of the 81 otolith samples. The age of each specimen was then estimated by Equation (3).

The fork length of the sample specimens is plotted against the point estimate of age in Figure 9. Because 13 of the 81 determinations were duplicates based on left and right otoliths from the same fish, and 4 of the remaining preparations had excessive coefficients of variation ($\geq$20%), only 64 points are presented. These data were fitted to the von Bertalanffy growth model (Ricker 1979) using a nonlinear regression routine (NLIN Procedure) (Statistical Analysis System 1979). In this three-parameter formulation, L_∞ signifies the asymptotic upper bound on growth in length, K is an instantaneous growth-rate constant, and t_0 is a scaling factor equal to the X-intercept. When the model was freely fitted to the data, an unrealistically low estimate of L_∞ resulted (Table 2, solid line in Figure 9). As part of a related study in

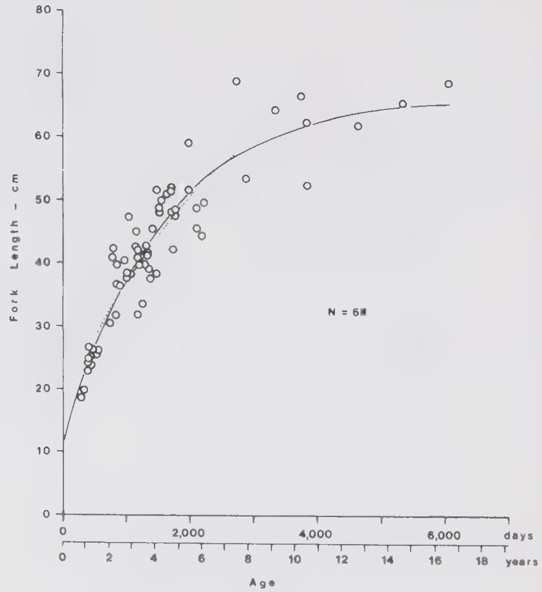

FIGURE 9.—Estimated growth curve for *Pristipomoides filamentosus*. Solid line represents a freely fitted von Bertalanffy curve whereas the L_∞ parameter was constrained to 78.0 cm in the fit of the dotted line.

TABLE 2.—Parameter estimates from the von Bertalanffy model fitted to 64 integrated age estimates of *Pristipomoides filamentosus*.

Parameter	Estimate	Standard error	Units
Freely fitted			
K	0.235	0.034	yr^{-1}
t_0	−0.807	0.298	yr
L_∞	66.4	28.15	cm
Constrained (L_∞ = 78.0 cm)			
K	0.146	0.010	yr^{-1}
t_0	−1.67	0.327	yr

which more than 2,500 opakapaka were measured, many fish exceeded 70 cm FL. Consequently, the 64 data points were refitted to the model with L_∞ constrained to a value of 78 cm FL, the largest specimen we have observed (Table 2, dotted line in Figure 9).

Analysis of Size-Frequency Distributions

The data presented in Figure 10 represent three length-frequency distributions of opakapaka sampled at French Frigate Shoals in the Hawaiian Islands. All three samples were taken on different dates but at the same position on the west side of the atoll (lat. 23°47′N, long. 166°22′W). In each distribution a large mode of small fish is plainly visible. If one accepts the premise that these small fish represent a single cohort of juveniles, these data afford the opportunity to estimate their size-specific growth rate by examining the progression of modes in time (Ricker 1975; McNew and Summerfelt 1978).

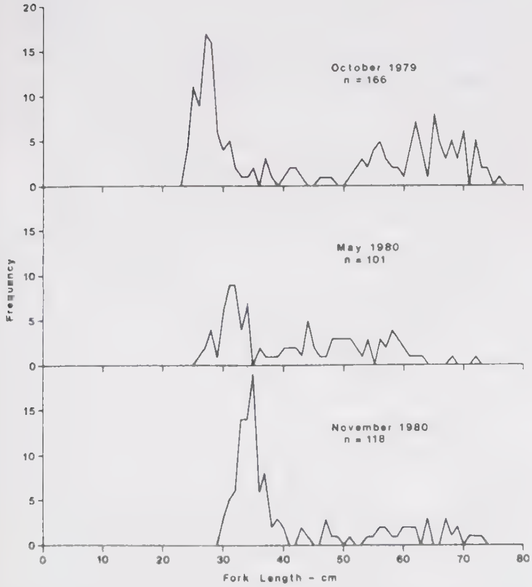

FIGURE 10.—Length-frequency distributions of *Pristipomoides filamentosus* sampled at French Frigate Shoals, Hawaiian Islands (lat. 23°47′N, long. 166°22′W).

The simplified calculations presented in Table 3 show that these fish grew, on the average, at the rates of 0.020 cm/d during the winter growth period (October-May), 0.022 cm/d during the summer growth phase (May-November), and an average 0.021 cm/d over the entire year (October 1979-November 1980). If we compute the expected size-specific (31 cm FL) growth rate of these fish, based upon the fit of the integrated otolith age data to the von Bertalanffy model (Table 2, Fig. 9), we predict growth rates of 0.023 and 0.019 cm/d for the freely fitted and the constrained versions of the model, respectively. These results compare favorably with the modal growth rates, further substantiating our age estimates.

TABLE 3.—Growth rate calculations for *Pristipomoides filamentosus* based on size-frequency distributions. Samples from French Frigate Shoals, Hawaiian Islands.

	Sample no		
	I	II	III
Date:	16 Oct. 1979	27 May 1980	3 Nov. 1980
Modal size (FL cm):	27.0	31.5	35.0
Samples compared	I-II	II-III	I-III
Elapsed time (d)	223	160	383
Change in length (cm)	4.5	3.5	8.0
Growth rate (cm/d)	0.020	0.022	0.021

DISCUSSION

Elsewhere we have shown that the increment thickness model presented here provides reasonably precise age estimates from a purely statistical standpoint (Ralston and Miyamoto 1981). The frequency distribution of coefficients of variation of T is centered on 6%, with 67 of the 81 values ≤10%. Thus, a typical preparation provides an age estimate for which the 95% confidence interval is about ±12% of the estimate. Furthermore, the regression technique is an effective means of accounting for variation in otolith growth rates. The frequency distribution of r^2 values for the 81 regressions had a median value of 78% (Ralston and Miyamoto 1981).

Several explicit and implicit assumptions, however, underlie the aging method presented here. It is important to address these at this time and to review to what extent they may or may not be justified. One important assumption is that it is appropriate to use the interpolative power of the regression Equation (2) to predict otolith growth rates in intermediate regions where increment microstructure is unclear. This assumption implies that similar processes occur in regions of the otolith that appear somewhat different superficially. We feel it is not an unreasonable assumption, however, because one can usually enhance the quality of a preparation by increasing the amount of time and care devoted to it, bringing out distinct increments in regions which otherwise would remain uninterpretable. For example, Radtke (footnote 3) has shown that the core area of opakapaka otoliths requires substantially more etching time than does the marginal zone. He improved the quality of his samples by employing differential etching times, a tedious but effective technique. Wild and Foreman (1980) used similar methods in their study. Presumably, the visual quality of a preparation is largely limited by the ability of the investigator to unveil its contents.

A second and more important assumption is that it is reasonable to extrapolate the growth of a sexually mature fish based on its individual pattern of growth prior to gonad maturation. Because all data gathered at otolith lengths >6,000 μm were deleted, age estimates obtained from Equation (3) are bound by this constraint. We have argued that otolith increments become equivocal chronometers past maturity, due to interrupted growth. Both Pannella (1971) and Wild and Foreman (1980) reached similar conclusions in their studies of red hake, *Urophycis chuss*, and skipjack tuna, *Katsuwonus pelamis*, respectively. Significantly, in the latter study growth interruptions were not evident in yellowfin tuna, *Thunnus albacares*, and almost all specimens were of immature size (Schaefer et al. 1963). Not only has maturation been implicated in interrupting otolith growth, but also reduced food (Irie 1960; Methot and Kramer 1979; Uchiyama and Struhsaker 1981) and low temperature (Irie 1960; Taubert and Coble 1977). It is apparent from these studies that any factor which arrests the growth of the whole fish, temporarily or otherwise, can lead to errors in the time chronicle of daily increments (Pannella 1980). Clearly, if the additional energy burden incurred at sexual maturity is substantial (sensu Gadgil and Bossert 1970), extrapolation beyond 6,000 μm may be an unrealistic exercise and growth rates of large fish may in fact be overestimated. However, it is pertinent to note that the proportions in opakapaka of both ovarian and testicular tissues relative to total body weight are not great, ranging from 1 to 4% among Stage III females and slightly less among males (Ralston 1981). Furthermore, most models of fish growth currently in use (e.g., von Bertalanffy and Gompertz models) do not treat maturity as a growth singularity, i.e., a time when the pattern of growth changes. In spite of their relative simplicity, these models have adequately described fish growth dynamics in a surprisingly large number of situations (Ricker 1979). Undoubtedly this is because fine scale departures from model growth (e.g., seasonal trends) are averaged out when treating a lifespan measured in years. Finally, the procedure we have used involves extrapolating, at most, 68% beyond the range of the data (6,000-10,000 μm). In most cases, the amount we extrapolated was far less. Nonetheless, this particular assumption is critical and yet remains unresolved. Additional research on this topic is essential.

At the other extreme, by applying a linear model to the data (Equation (2)), we have assumed that otolith growth rate is greatest as otolith length approaches zero. This is unrealistic (see, for example, Pannella 1974; Brothers and McFarland 1981). The average width of increments actually decreases very near the focus (Fig. 2). We evaluated the extent of bias introduced by this computational simplification, however, by comparing age estimates derived from both analytical (Equation (3)) and complete numerical integration of all the otolith growth-rate data, broken down by 100 μm size classes. The largest absolute difference between the two types of age estimates was 18 d. This was for the youngest of fish, as might be expected, and indicates that the analytical method provides a poor approximation for fish <1 mo old. However, because our results are intended to describe growth over the entire size range of opakapaka, measured on a time scale of years, and because the difference between the two estimates becomes progressively smaller among the larger fish, we consider this a negligible error.

A final assumption is that one increment forms each day in preproductive individuals. We have presented evidence that validates this assumption, at least for fish 30-34 cm FL, in the form of in vivo marking of otoliths with tetracycline. Furthermore, evidence from the field (Fig. 10) also strongly supports this conclusion, again for immatures (27-35 cm FL). A final assessment of this assumption can be made by comparing the growth of opakapaka, as developed here, with studies available in the literature on lutjanid growth.

Researchers have long recognized the interdependence of growth parameters. Beverton and Holt (1959) presented values of K and L_∞ computed from the von Bertalanffy growth model and noted an inverse relationship between these parameters. Similarly, Cushing (1968) presented graphs relating growth parameters for several large taxonomic categories (e.g., Clupeoidei, Gadiformes, Salmonoidei, etc.). Pauly (1979) has attempted to quantify the relationship between asymptotic weight (W_∞ or the weight of an individual at length L_∞) and K by developing the concept of the auximetric grid. He has argued that the logarithm of the product of K and W_∞ is relatively uniform for families of fishes. That is

$$P = \log_{10} (KW_\infty)$$

where P can be considered characteristic of taxa.

A review of the lutjanid growth literature allowed us to estimate P for lutjanids by computing the arithmetic average of the eight P values presented in Table 4 ($\bar{P} = 3.03$). An estimate of the asymptotic weight of opakapaka is 7,670 g (Ralston 1981). Using these two figures, we calculate an estimate of K for opakapaka to be 0.140 yr^{-1}. This figure compares very favorably with the estimate of K obtained from the constrained fit of the von Bertalanffy model to otolith data from immature fish presented earlier (0.146 yr^{-1}). The results of our marking experiments, length-frequency data, and literature comparisons all support the conclusion that increments are formed daily in subadult opakapaka (up to 3 yr old).

After considering all of the assumptions that underlie our analysis, we conclude that the results presented in Figure 9 accurately reflect the growth of opakapaka. Other investigators (Moffitt 1980; Radtke footnote 3) have presented growth curves for opakapaka, also based on otolith microstructure, but which show somewhat faster growth, especially for large, mature fish. Both studies were based upon complete counts of growth increments. We attribute the differences between our estimates and theirs to growth interruptions confounding the otolith time record in adults. These earlier studies neglected to entertain this possibility, an oversight which could lead to serious underestimates of age.

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TABLE 4.—Growth relationships among the Lutjanidae with application of the auximetric grid (Pauly 1979).

Species	K (yr^{-1})	W_∞ (g)	P[1]	Source
Lutjanus apodus	0.180	3,774	2.83	Munro 1974
L. bohar	[2]0.106	9,100	2.99	Talbot 1960
L. campechanus	0.162	13,480	3.34	Nelson and Manooch 1982
L. johnii	[2]0.135	—	—	Druzhinin 1970
L. malabaricus	[2]0.064	13,600	2.94	Druzhinin 1970
L. purpureus	0.090	—	—	Menezes and Gesteira 1974
L. sanguineus	0.142	10,597	3.18	Lai and Liu 1974
	0.148	12,469	3.27	Lai and Liu 1974
L. synagris	[2]0.101	—	—	Druzhinin 1970
Ocyurus chrysurus	0.250	3,600	2.95	Munro 1974
Rhomboplites aurorubens	0.198	2,800	2.74	Grimes 1978

[1] $P = \log_{10} (KW_\infty)$
[2] Estimated from Walford plots of size-at-age data

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POPULATION ASSESSMENT OF THE GRAY WHALE, *ESCHRICHTIUS ROBUSTUS,* FROM CALIFORNIA SHORE CENSUSES, 1967-80

STEPHEN B. REILLY,[1,2] DALE W. RICE,[1] and ALLEN A. WOLMAN[1]

ABSTRACT

Estimates of abundance by year were developed for the California-Chukotski stock of gray whales, from a 13-year consecutive series of shore censuses, conducted near Monterey, Calif. Annual estimates of population size range from a low of 10,414 for 1971-72 to a high of 17,577 for 1979-80. Standard errors are about 10% of population estimates. During the 13 years censused, the population increased annually by 2.5%, concurrent with a 1.2% harvest in the Soviet subsistence fishery, indicating a 3.7% net annual productivity.

Seasonal migratory timing was relatively constant during the study period. Gamma probability density function models of the annual migrations past Monterey had an overall mean day of 9 January, with a range from 8 to 19 January. A slight depression in mean hourly count for 0070-0800 h, during 1978-79 and 1979-80, contrasted with a constant mean hourly count through 10 daylight hours during the previous 11 years. Aerial surveys of the offshore distribution of southward migrating whales during 1979-80 agreed closely with those reported for 1978-79, indicating that 40% pass within 1 mile (1.6 km) of shore and 90% within 2 miles (3.2 km). In the shore censuses, about 20% of the passing whales were missed due to their distance offshore.

The estimation of population size for large whales has traditionally been based upon information derived from exploitation, e.g., catch per unit effort, mark-recapture, or related data (Allen 1980). Because of the recent decline in exploitation of marine mammals, assessment techniques based upon sighting surveys are increasing in importance (Eberhardt et al. 1979). The annual migration of the California stock of gray whales, *Eschrichtius robustus* (Lilljeborg 1861), makes it especially well suited to assessment by means of sighting surveys. Assessment studies on this stock can potentially aid in the development of sighting survey field and analysis techniques, especially those in which the observer is stationary and the population mobile. This paper presents some recent developments in the use of shore-based census data for whale population assessment, and the results of the 1979-80 gray whale census. Revised population estimates for the previous 12 annual censuses are also reported, along with a consideration of change in population size during the period 1967-80.

Each year during the northern winter the California stock of gray whales migrates from feeding waters in the Bering and Chukchi Seas, south along the west coast of North America, to calving areas in Mexican waters (Fig. 1); the stock returns to the Arctic in the spring (Rice and Wolman 1971). In many places along the route, the whales pass very close to land (Gilmore 1960; Pike 1962; Rice and Wolman 1971; Rugh and Braham 1979). Consequently, it is feasible to census the migrating whales visually from strategic points along the shore.

Early shore-based censuses were summarized by Reilly et al. (1980). Systematic censuses of southward migrating gray whales were initiated during the winter of 1967-68 at both Point Loma (lat. 32°40′N; 130 m above sea level) in San Diego, Calif., and at Yankee Point (lat. 36°29′N; 23 m above sea level) near Monterey, Calif. The San Diego count was conducted intermittently until 1977-78, for a total of 5 yr. The San Diego data were not analyzed in this study because an unverified proportion of the population passes far offshore south of Point Conception (Rice 1965) and because the migration route may have been influenced by increased boat traffic (Rice 1965; Reeves 1977). The Monterey census was conducted each year for 13 yr up to and including 1979-80. Beginning in 1975-76 the counting station was moved 3.7 km south to Granite Canyon (21 m above sea level) due to real estate development of the Yankee Point site. The Monterey data were used as the basis for this study, because they form a continuous time series and are less complicated by coastal geography and boat traffic than the San Diego data.

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[1] National Marine Mammal Laboratory, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

[2] National Marine Mammal Laboratory, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, Wash.; present address: Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038.

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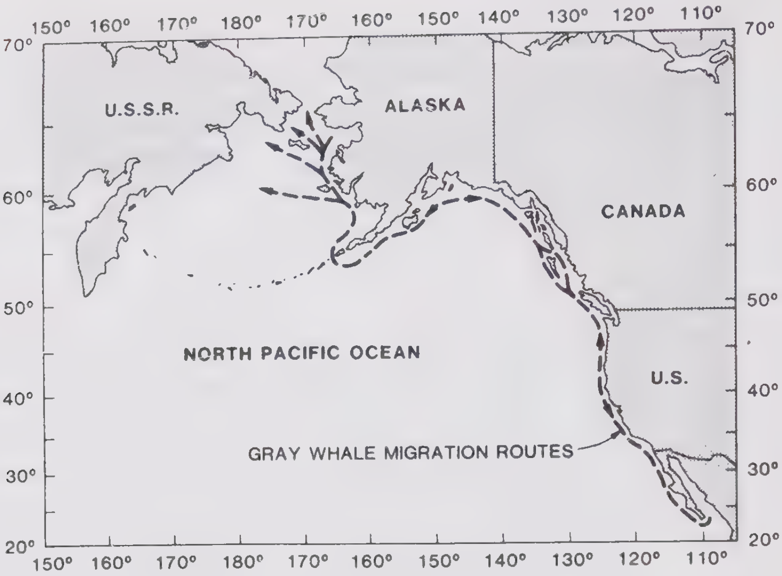

FIGURE 1.—The approximate migration route of the California stock of gray whales.

To estimate total abundance by extrapolating from recorded counts of passing whales one must determine the following:

1) What proportion of the population, if any, passes beyond sight of the observers? Does this change with time or experience? How does the observer's accuracy in estimating the distance to passing whales vary with distance?
2) Are there diel variations in migration rate? How can daylight counts be used to estimate the number of whales passing at night?
3) How do weather (visibility) conditions affect census results?
4) Does the observer's ability to count the number of individuals within a passing group vary with group size?
5) Are the initiation and termination of the migration fully represented in the data?

During the 1978-79 southward migration we conducted two types of verification experiments aimed at addressing the questions of points 1 and 4 above. These were reported in detail in Reilly et al. (1980). In one experiment we tested 12 observers simultaneously for accuracy in estimating distances to and numbers within 50 events in which whales passed the Granite Canyon station. The observers estimated the distance offshore to within one of seven predefined distance intervals, as during the actual annual censuses (see Methods). We found significant heterogeneity between observers for both distance and count estimates. Given this heterogeneity, there were also consistent biases recorded: In placing whales to within correct intervals out to 1 mi (1.6 km) and beyond 1.5 mi (2.4 km), and in estimating the true number of individuals present in groups of one whale, and four or more. Further analysis of this data (Reilly 1981) indicated that "experienced" observers were on average no more accurate than inexperienced observers, but somewhat more precise.

A second experiment was conducted during 1978-79 to characterize the width of the migration corridor offshore from the Monterey counting stations (Reilly et al. 1980). A small aircraft flew a series of transects perpendicular to the coast in the vicinity of the stations, recording locations of sighted whales (Fig. 2). The results indicated that, contrary to previous assumptions and characterizations of 95% of the population passing within 1.6 km (Rice and Wolman 1971; Sund and O'Connor 1974), we found only about 40% within 1.6 km, with significant numbers passing offshore between 1.6 and 4.5 km. This experiment was repeated during 1979-80, with results reported here.

Regarding night migration rate (point 2 above), after a review of all available information, we accepted an assumption of a constant 24-h rate. Contrary to the earlier report of Ramsey (1968), we found no evidence of a diurnal fluctuation from the shore census data. During the 1979-80 migration a new (prototype) infrared image sensor, supplied by the U.S. Department of Defense, was tested at Granite Canyon. As with previously tested night-vision devices (Reilly et al. 1980), it proved unsatisfactory.

The possible effect of visibility conditions on cen-

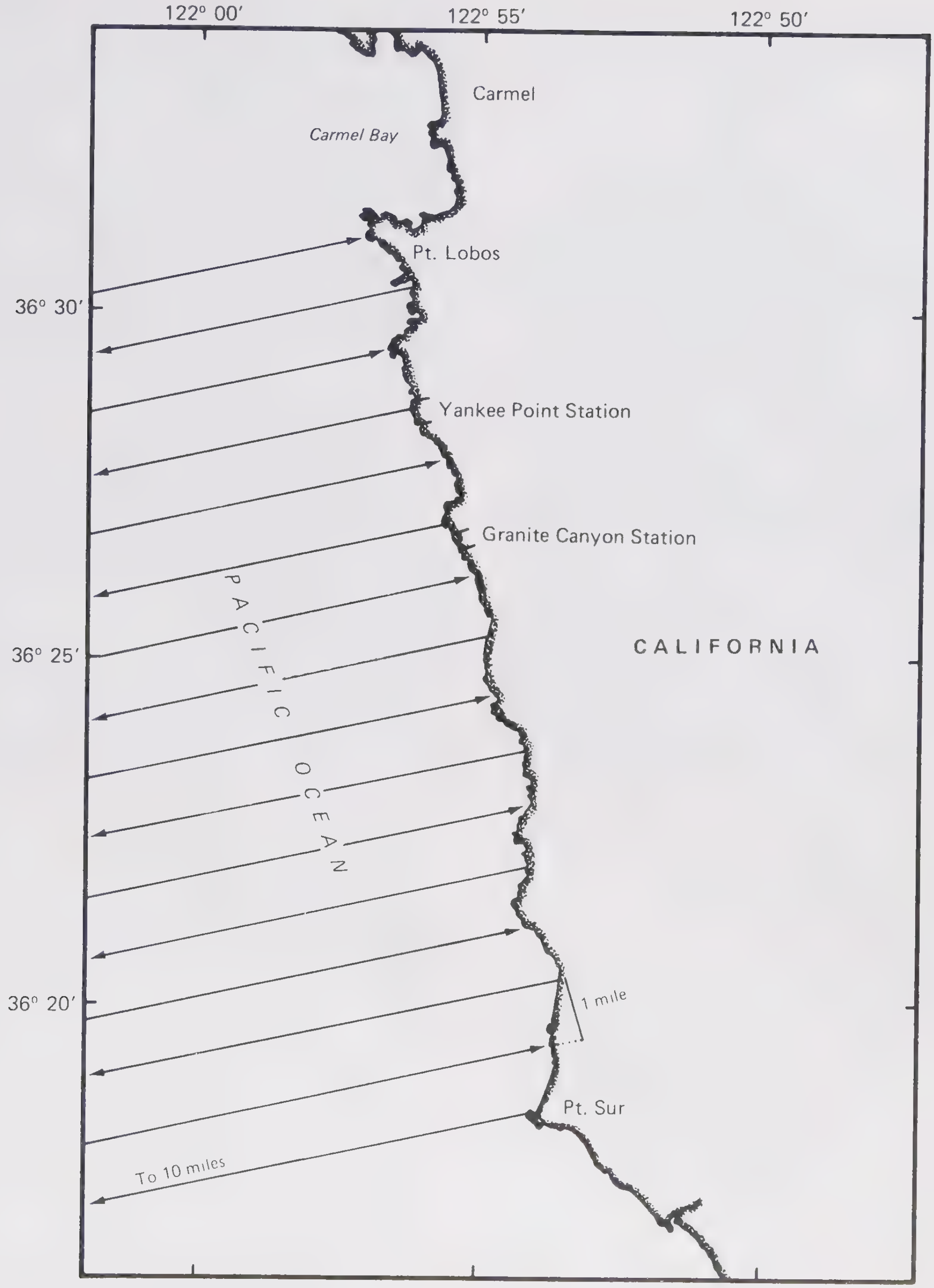

FIGURE 2.—The California coast south of Monterey, showing census stations and aerial transect lines for gray whale study.

sus results was not addressed in Reilly et al. (1980). We report here a quantitative appraisal of this effect, and account for it in our abundance estimation.

METHODS

Field Methods: Shore Census

The exact seasonal duration of the annual census changed only slightly from year to year, but it usually began on or before 10 December and ended on or after 6 February (59 d). The watch was conducted between 0700 and 1700 h, 7 d a week, by two observers who alternated 5-h shifts.

The observers watched to the north for southward swimming whales to come into view. At first sighting of a whale or group of whales the time was recorded and an initial estimate was made of the number of whales in the group. The whales were kept under observation until they were directly offshore from the station, usually about 0.5 h later. At that time a final estimate of the number present was recorded, along with the time and an estimate of the distance of the animals offshore. Distance estimates were classified in seven intervals: 0-0.25; 0.25-0.50; 0.50-0.75; 0.75-1.0;1.0-1.5; 1.5-2.0; 2.0+ mi. Beaufort Sea state, wind direction, and notes on visibility conditions were recorded continuously throughout the day. Binoculars (7 × 50) were used regularly. Beginning in 1978-79, visibility conditions were assigned one of six ordinal categories (Table 1) for each pod observed. For data prior to 1978-79, visibility conditions were classified to within these categories during the analysis, based upon information recorded systematically during the censuses.

TABLE 1.—Gray whale census—Granite Canyon visibility codes.

Code	Condition	Description
01	Excellent	Clear day, or high clouds. No glare. Horizon visible. Effective sighting distance = 3+ mi.
02	Very good	Clear or some cloud cover. Some glare, surface ripple. Effective sighting distance = 2-3 mi.
03	Good	Some fog, haze, low clouds. Some interference from chop, surf, or glare. Effective sighting distance = 1-2 mi.
04	Fair	Fog, full overcast, light rain, haze with glare. Frequent whitecaps. Effective sighting distance = 0.5-1 mi.
05	Poor	Moderate rain or fog, large surf, bad glare, etc. Effective sighting distance = 0.25-0.5 mi.
06	None	Combination of conditions make it very difficult or impossible to see even the closest (within 0.5 mi.) whales. Heavy rain, dense fog, near darkness, etc.

Analysis Methods: Shore Census

Occasionally during the censusing, only one of the standard two sighting times per group (when first seen and when directly offshore) was recorded. Frequently when an observer came on duty at 0700 h there were whales directly offshore and no "north time" was recorded. In addition, at the end of the day at 1700 h, whales which had not yet passed directly in front of the station were often sighted to the north, and no "south time" was recorded. To correct for missing time records, a mean difference between the two times was calculated for each observer individually. Missing time records were then generated from this average, and the single time record available. The time when the animals were directly offshore was then used to categorize data for time of day analyses. Only sightings with this time falling between 0700 and 1700 h were used for abundance estimation.

The results of the 1978-79 and 1979-80 half-day observation periods were investigated by analysis of variance (ANOVA) for differences between observers and between morning vs. afternoon periods on rate of recording animals, as was previously done (Reilly et al. 1980) for the 1967-68 through 1977-78 data. We also examined the two most recent censuses for possible changes in hourly rates of recorded counts, as done previously for the 1967-68 through 1977-78 data. Again, we looked for significant depressions in the counts both at the ends of the 5-h observer periods (as an indication of observer fatigue) and at the beginning and end of the day (as an indication of daylight-mediated change in migration rate).

For any migratory species which can be censused feasibly from a fixed point, the distribution of daily counts, transformed to proportions for each migration, can be viewed profitably as a time-density distribution and modeled by various probability density functions (Mundy 1979). We previously assumed a normal distribution (Reilly et al. 1980) for all years pooled. Problems with this approach were that mean days between years were not equal and that a slight but consistent skewness occurred causing lack of fit. Consequently we have replaced the normal distribution with the more flexible gamma distribution (Pearson's Type III; Bury 1975) and modeled each year separately. The time-density model for each migration was then employed in three ways:

1) To estimate the number of whales having passed the station before the first and after the last day of the census (the "tails").
2) As a standard for comparison with observed daily results, in a determination of if, and to what degree, conditions associated with the six visibility categories affect census results.

3) To estimate the proportion of the population passing the census station on days for which the visibility conditions were worse than a critical value, as determined by the results of the visibility analysis (2).

The data on pod-size estimation from all years were examined both for differences between years and for a pattern in distance from shore.

The offshore distance frequency distribution of observations was investigated for significant differences between the two locations, as a preliminary to post facto application of correction factors for whales missed offshore.

Field Methods: Verification Experiments

The aerial transects to determine the offshore distribution of the migratory corridor were repeated in 1979-80 following our previous methods (Reilly et al. 1980). We flew a Cessna 172[3] aircraft at 305 m (1,000 ft) altitude, at a speed of 145 km/h (90 mi/h), along a series of predefined tracklines (Fig. 2). These lines were situated along a 25 km stretch of the coast which included both the Yankee Point and Granite Canyon census stations. Distances of whales from shore were calculated from the timed difference between their position and the shore edge, and the plane's speed. During 1979-80 we flew a total of 13 flights for 34 h, in periods of good to excellent visibility. Flights were continued until a number greater than the minimum sample size of whales was obtained (330) for 90% precision in correctly classifying the population into the seven distance intervals used in the shore census (Reilly et al. 1980). Sample-size determination was based upon Cochran's (1977:74-76) formulae for sampling for proportions. Data from the 1974-75 shore counts were used as a presample of the proportions expected within the distance intervals from shore. The seven-interval experimental design also presented the opportunity to analyze the data in a pooled, less demanding interval scheme, with resulting higher precision in estimating the within-interval proportions.

Additive bias corrections were previously determined from the results of the observer bias experiments regarding estimation of the number of whales present in passing groups. Specifically for estimates of group size n (see Appendix 1 for explanation of notation)

$$E[n] = \hat{n} + b_n = \begin{cases} n + 0.350 & n = 1 \\ n + 0.00 & n = 2,3 \\ n + 0.333 & n \geq 4 \end{cases} \qquad (1)$$

with variances as in Appendix 2.

Analysis Methods: Verification Experiments

Aerial sightings were analyzed for effects on offshore distance estimates from: differences between the two individual observers; the side of the plane from which the whales were seen; and the period of day (morning or afternoon flight) by ANOVA. The distance distributions from the 2-yr surveys were tested by χ^2 (chi-square) for the possibility of pooling.

To address the misclassification bias suggested by the results of the 1978-79 experiments, the data from those experiments were reanalyzed by using a less demanding classification scheme of three broad intervals: 0-0.75 mi (1.2 km); 0.76-1.5 mi (2.4 km); 1.6 mi + (2.6 km). From this characterization, a series of reclassification parameters (probabilities) were calculated, ρ_{ab}, being the proportion of whales estimated to be within interval a, that were determined to be actually passing within interval b. The actual census data, structured in the same three intervals, were restructured by application of these parameters as

$$\hat{m}_b = \sum_a (m_a \rho_{ab}), \qquad (2)$$

where m_a includes the whales originally classified into interval a, and $\hat{m}_b$ comprises the whales redistributed into interval b, which were originally (erroneously) estimated to be in a. For example, for $a = 1$ and $b = 1$, sightings correctly classified into interval 1 are summed into the new $\hat{m}_{b=1}$. For $a = 2, b = 1$, sightings incorrectly classified during the censuses into interval 2 are reclassified, or summed, into $\hat{m}_{b=1}$. In the case of $a = 2, b = 1, \rho_{21} = 0.2367$ of the whales originally put in interval 2 would be placed into interval 1. The redistributed census data were then compared with the "true" distribution from the aerial surveys. As a simple correction factor, the ratio of the cumulative proportions seen within 2.4 km (1.5 mi) was calculated for each year (k):

$$h(k) = C_s / C_p. \qquad (3)$$

A necessary assumption of this method is that at least during periods of good or better visibility, all groups of whales passing within 2.4 km (1.5 mi) were recorded.

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[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Analysis Methods: Estimation of Abundance

In fitting the probability density functions to the census data, the unit used was the estimate of the proportion of the population passing during a 24-h day. The number passing on day j was estimated as

$$\hat{n}_j = (\Sigma E[n]/t_j) \cdot 24, \tag{4}$$

where $E[n]$ is the expected value of n, i.e., the estimate of the number per group, corrected for bias as in Equation (1). The relative proportion passing on day j was estimated as

$$\hat{p}_j = \hat{n}_j/\Sigma\hat{n}_j. \tag{5}$$

Model parameters were first estimated for each year using all data points regardless of recorded visibility conditions. Data were fit by the two-parameter gamma model

$$f(j;\alpha,\beta) = \frac{1}{\alpha \cdot \Gamma(\beta)} (j/\alpha)^{\beta-1} \exp\{-j/\alpha\} \tag{6}$$

for each migration separately. The parameters of the gamma distribution, their variances and covariance, were estimated by the method of maximum likelihood (Chapman 1956; Greenwood and Durand 1960). Equality of parameters between years was tested by the F statistic (Chapman[4]),

$$F = \frac{\Sigma\,(x - \bar{x})^2/n - 1}{\Sigma\,\mathrm{var}\,(x)/n} \tag{7}$$

for $x = \alpha, \beta$.

The distribution of $\hat{p}_j$ for each year was then used to determine the effect of visibility conditions on census results. An average visibility condition was calculated for each day from all of the recorded codes (Table 1). The difference (residual) between the observed and predicted relative proportions for each day was also calculated. An ANOVA was performed on the residuals with visibility categories as groups, along with multiple range tests (Duncan's, Student-Newman-Kuels, Scheffe's). These results were used, along with an examination of the mean squared errors for each category, to set a critical level of visibility conditions beyond which there was significant interference with accurate censusing. The data were then refit by the gamma distribution using only days with visibility codes less than the critical value as points. The new set of daily predictors ($\hat{p}'_j$) from the fitted gamma model were used in the further estimation procedures.

Then, as an alternate to Equation (2), the abundance for day j was

$$\hat{n}_j = \begin{cases} [(\Sigma E[n])/t_j]\;24 & : \text{vis} \leq \text{critical value} \quad (8a) \\ \hat{p}'_j\;(\Sigma\hat{n}_j) & : \text{vis} > \text{critical value.} \quad (8b) \end{cases}$$

That is, for days with visibility conditions less than or equal to some critical level (with levels defined as in Table 1) the average hourly sighting rate, corrected for counting bias, multiplied by 24 h, was used as the estimate of the total number of whales passing. For days with visibility conditions worse than some critical value, the estimate of the number passing came from the expected proportion for the day (from the gamma distribution model of migratory timing for that year, p'_j) multiplied by the sum of the daily estimates from the first fitting of the gamma model.

For estimating the "tails" of the migration, a slight modification of the method of Mundy (1979) was used. This method was developed to predict total run size for salmon from intermediate results of counts, given that migratory timing can be modeled. The total "run" N_j was predicted by minimizing the least squares error function

$$\text{err} = \sum_j \left(\theta_j - \frac{\Sigma n_j}{N_j}\right)^2 \tag{9}$$

which was solved for $\hat{N}_j$ (N estimated by data cumulative to day j) by

$$\hat{N}_j = \sum_j (\Sigma n_j)^2/\Sigma n_j\theta_j. \tag{10}$$

Here Mundy uses θ_j as the cumulative proportion expected to have passed by day j, and we define θ_j as that quantity less the predicted proportion missed before the first day of each census.

The final form of the abundance estimate for each year k was then,

$$N_k = \{\sum_j (\Sigma n_j)^2/(\Sigma n_j) \cdot \theta_j\} h(k). \tag{11}$$

The variance for Equation (11) was estimated in two ways. The first, S_0^2, outlined in Appendix 2, was derived from the component variances of the parameters used in the model, employing the Delta Method (Seber 1973). In the second method the data were subsampled in five 2-h samples/d. The five estimates for the year were then calculated using Equation (11). A simple variance of these estimates about the mean estimate (S_R^2) was then calculated. Variances were compared for equality ($H_0{:}S_R^2 = S_0^2$) by the test statistic

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[4] D. G. Chapman, Director, Center for Quantitative Science, College of Ocean Fishery Sciences, University of Washington, Seattle, WA 98195, pers. commun. March 1980.

$$\chi^2 = \frac{(n-1)S_R^2}{S_0^2}, \tag{12}$$

where χ^2 is distributed approximately as chi-squared (Freund 1962:371) with rejection regions $\chi^2 > \chi^2_{\alpha/2,\,n-1}$ or $\chi^2 < \chi^2_{1-\alpha/2,n-1}$.

Analysis Methods: Trends in Population Size

In order to test for a trend in population size during the 13-yr study period, two models were chosen for regression analysis. This first model was simple linear regression, the second was a weighted $\log_e$ model:

$$N_t = N_0\, e^{rt}, \tag{13}$$

where N_t is population size in year t, N_0 is year zero, or 1967 for the shore census time series. Equation (13) was fit linearly as

$$\ln N_t = \ln N_0 + rt, \tag{14}$$

with weights calculated as an inverse function of the estimated variance of N_t in the log model:

$$\begin{aligned} \mathrm{Var}(\ln N_t)\ \ & [f'(N_t)]^2 \mathrm{Var}(N_t) \\ &= \mathrm{Var}(N_t)/N_t^2 \\ &= w_t^{-1}. \end{aligned} \tag{15}$$

RESULTS

Shore Census Data Base

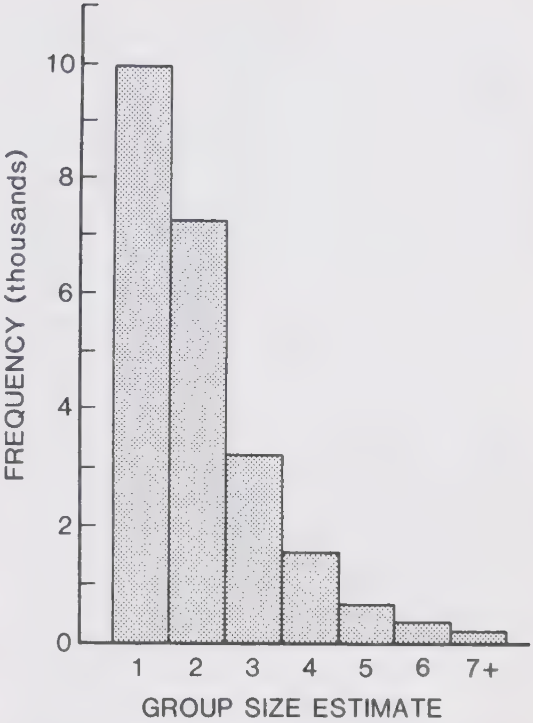

FIGURE 3.—Frequencies of group size estimates from Monterey gray whales census, 1967-68 through 1979-80, n = 23,678 observations.

TABLE 2.—Mean pod size estimates by year for the Monterey gray whale censuses, 1967-68 through 1979-80. Group membership identifies placement by multiple range tests into one of three nonsignificantly different subgroups.

Year	Mean pod estimate	SD	n	Group membership
1967-68	2.4970	3.5520	1239	3
1968-69	2.1471	2.2550	1509	2
1969-70	2.0900	2.2790	1643	2
1970-71	2.0330	1.6110	1652	2
1971-72	2.1630	1.8700	1272	2
1972-73	2.1400	1.6780	2041	2
1973-74	2.0990	1.7980	1859	2
1974-75	2.0710	1.9170	1855	2
1975-76	2.0620	1.7210	2086	2
1976-77	2.0660	1.5930	2296	2
1977-78	1.8250	1.2470	1996	1
1978-79	2.0040	2.3750	1960	2
1979-80	2.1030	1.7120	2341	2
Overall	2.0855	1.9736	23,799	

Analysis of variance

Source	df	ss	ms	F
Between groups	12	385.7561	32.1463	8.283[1]
Within groups	23,736	92,119.1877	8.8810	
Total	23,748	92,504.9438		

[1] Significant at $\alpha = 0.05$

A histogram of group sizes as recorded from the 13 annual censuses is presented in Figure 3. The overall mean was 2.086 ($S^2 = 1.974, n = 23{,}749$). The mean group sizes by year are listed in Table 2. An ANOVA indicates that there are significant differences between the mean pod sizes recorded by year ($F = 8.282 > F_{12,\infty,0.05}$). Multiple range tests (Duncan's, Student-Newman-Kuel's, Scheffe's) show that 1967-68 and 1977-78 are different from each other and the rest, while all the others are homogeneous. In the 1967-68 census the unusually high mean is attributable to one of the two observers that year. His individual mean pod was 3.123 ($S^2 = 2.651$), and was significantly different from the other observer that year, whose mean was 1.886 ($S^2 = 1.959{:}t = 24.528 > t_{\infty 0.05}$). In 1977-78 however, the two observers did not differ significantly from each other in mean pod size estimated (1.842, 1.829, $t = 1.1442 < t_{\infty,0.05}$) and, consequently, the difference of this year's data from others cannot be credited to one aberrant observer.

There was a significant increase in mean group size as a function of distance from shore (Fig. 4) ($F = 97.28 > F_{5,231}$). A significant linear increase in the pooled data (Fig. 4) was also noted in 10 of the 13 individual years. In the remaining 3-yr data (1968-69, 1972-73, 1978-79), the average pod size peaked at about 0.6-0.9 km (1-1.5 mi) from shore, and decreased thereafter. This may be a real between-year difference in whale behavior, but is more likely a function of the varying abilities of the observers themselves.

There are highly significant differences between years in the frequency of observations recorded within offshore distance intervals ($\chi^2 = 2,340$, df = 24). For this analysis, a pooled three-interval distribution was used in light of the observer bias tests discussed above. Within both the Yankee Point location subset of years and the Granite Canyon subset there also exists significant heterogeneity in the offshore distribution ($\chi^2 = 1,077$, df = 14; $\chi^2 = 1,025$, df = 8, respectively). Given this, a difference between locations pooled over years ($\chi^2 = 239$, df = 2) is not surprising and also not particularly meaningful. Consequently, given the range of interyear variation, we cannot adequately test for interlocation differences in the migratory corridor and therefore have applied distance estimation corrections equally to data from both locations.

Within each year, the distribution of distance estimates was tested for a within-season change, since our verification experiments were conducted during roughly the middle third of the migration. For this, the data were divided into early (10-29 December), mid (30 December-18 January), and late (19 January-6 February) time periods. As with the first 11-yr data (Reilly et al. 1980), the 1978-79 and 1979-80 distributions have no seasonal differences indicated by contingency table analysis ($\chi^2 = 8.54, 7.13, < \chi^2_{4,0.05}$), but do have significantly different mean distance observations ($F = 16.34, 26.91 > F_{2,\mathrm{X},0.05}$). Consequently, as with the first 11 yr, only data from the middle third of the migration were used for comparison with aerial results in Equation (3).

No significant period differences were indicated for the 1978-79 and 1979-80 censuses, in the ANOVA testing for effects on numbers of whales recorded per 5-h shift, from variation between observers and from period (morning or afternoon). Similar results were obtained in the comparison of observers within each year ($F = 1.242, 2.003, F_{1,118}$). The data were therefore considered homogeneous for pooling over these factors.

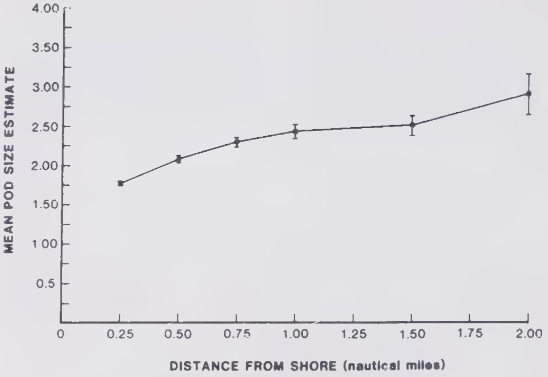

FIGURE 4.—Mean pod size estimates by distance from shore, with 95% confidence limits, from 13 annual gray whale census, 1967-68 through 1979-80, $n = 23,678$ observations.

The results from 1978-79 are somewhat different than the results from the first 11 yr, in the rate of whales recorded per hour of day. The mean counts show significant differences in an ANOVA ($F = 3.717 > F_{9,\infty,0.05}$) which are due to the depressed value for 0700-0800 h (Fig. 5). Multiple range tests (Duncan's, Student-Newman-Kuel's) indicate that the hourly means (other than that for 0700-0800 h) are homogeneous.

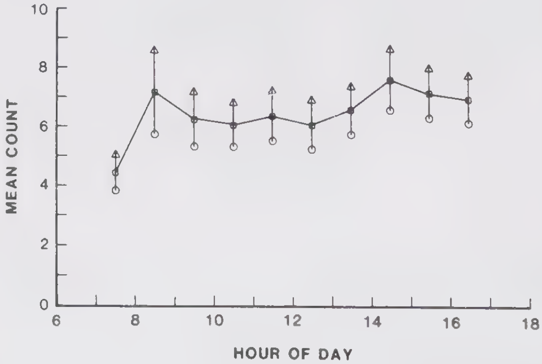

FIGURE 5.—Mean count of gray whales passing Granite Canyon Station by hour of day, with 95% confidence limits. 1978-79 and 1979-80 pooled, $n = 120$ d.

Modeling of Migratory Timing

Table 3 lists the parameters of the gamma distribution as calculated for all 13 yr, along with the mean days ($\simeq \alpha\beta$) and standard deviations ($\sqrt{\alpha} \cdot \beta$) of the annual migrations. As previously discussed, the

TABLE 3.—Parameters of the gamma models of migratory timing for each of the 13 annual gray whale censuses. $S_{\bar{x}}$ is the standard error of the scaled mean day.[1] α, β, their variances, and covariances are maximum likelihood estimates, as in Greenwood and Durand (1960).

Year	Mean day	$S_{\bar{x}}$	α	var(α)	β	var(β)	cov(α,β)	n[2]
1967-68	11 January	10.05	6.0679	1.6862	3.7900	0.5758	42.4097	41
1968-69	19 January	11.13	4.8378	0.8033	6.4070	1.3028	59.0233	44
1969-70	08 January	11.68	5.0684	0.8400	6.3140	1.2042	60.8971	46
1970-71	10 January	13.09	6.6379	1.3877	4.9716	0.7036	61.9997	65
1971-72	14 January	14.58	7.9561	2.5758	3.5195	0.4367	51.3318	41
1972-73	16 January	15.16	8.8199	2.6032	3.7417	0.4094	60.7978	57
1973-74	14 January	14.47	7.5301	2.0797	4.3812	0.6278	61.4829	49
1974-75	12 January	13.12	5.6951	1.1374	5.7946	1.0430	62.5312	54
1975-76	09 January	13.09	6.0154	1.3424	4.9872	0.7662	56.3723	39
1976-77	12 January	13.17	5.6979	1.1356	5.9680	1.1456	64.5253	55
1977-78	09 January	14.10	6.7340	1.6036	4.6039	0.6833	57.9679	21
1978-79	11 January	14.38	7.1149	1.7302	4.6383	0.6598	61.7334	60
1979-80	14 January	12.82	5.1287	0.9149	7.2144	1.6887	70.8288	48

[1] The mean day is ($\alpha\beta$), scaled so that 10 December = 1.

[2] Number of days with visibility conditions of fair or better, used as points for the fit.

means and variances are not equal statistically. Following adjustment on the time scale so that mean days align, however, we cannot reject the hypothesis of equality of parameters for the gamma distribution between years. For the α's, $F = 1.33 < F_{12,\infty,0.05}$. For the β's, $F = 1.54 < F_{12,\infty,0.05}$, where the F statistics were calculated as in Equation (7). Figure 6 illustrates data on daily proportions of the population passing Monterey, pooled over the 13 yr, as fit by the cumulative gamma. The use of the gamma represents a marked improvement in fit over the normal distribution, which we employed previously (Reilly et al. 1980). The error sum of squares from gamma model was 0.0179, while that from the normal fit to the same data was 0.1998, one order of magnitude greater.

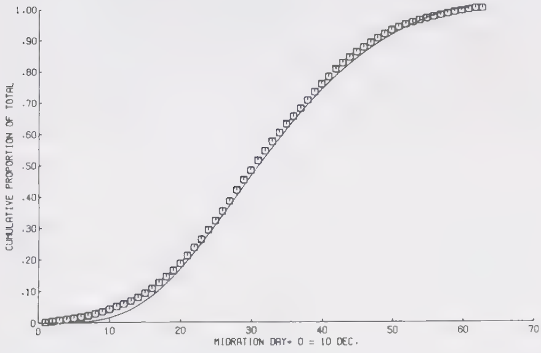

FIGURE 6.—Cumulative proportions of total count of gray whales by day (averaged) fit by the cumulative gamma function. Error sum of squares = 0.0179.

Effect of Visibility Conditions on Censusing

There are significant differences between visibility categories in the residuals (differences) of the observed from expected daily proportions of the population passing the census site (ANOVA: $F = 63.99 > F_{5,749,0.05}$). Three separate multiple range tests (Duncan's, Student-Newman-Kuel's, Scheffe's) gave the following nonsignificantly different subgroups of visibility codes, arranged in order of increasing magnitude of residuals:

1. visibility = 1, 2, 3
2. visibility = 1, 3, 4
3. visibility = 5
4. visibility = 6.

A simple interpretation of these results is that for conditions ranging from 1 (excellent) to 4 (fair), there is no significant interference from weather in shore censusing of gray whales. A plot of the mean squared residual for each category (Fig. 7) graphically illustrates this. Consequently, for days with average

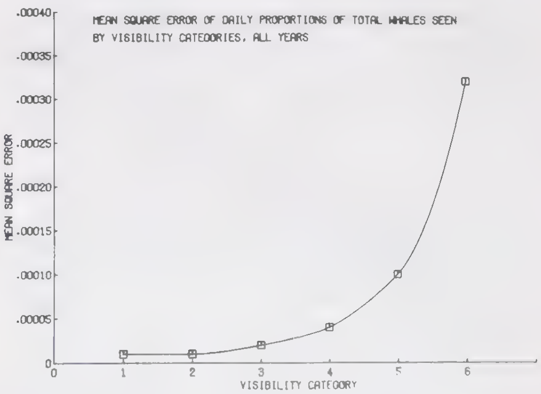

FIGURE 7.—Mean squared errors from comparison of daily proportions of total number of whales seen per season to proportions predicted by the gamma distribution, by visibility categories, all 13 yr included.

visibility of fair or better (<4) the total count for the day was estimated by Equation (8a), while for days with visibility of poor or worse (>4), it was estimated by Equation (8b). (The number of fair or better days recorded each year are listed in Table 3.)

Verification Experiments

The distance estimate data from the 1979-80 aerial survey were found to be homogeneous for pooling over sides of the plane, observers, and flight periods (Table 4). Further, the two separate years aerial data were homogeneous, and therefore pooled to form the model distribution (Table 5). This offshore frequency distribution was used as a standard for comparison with the annual observed distributions, as in Equation (3).

The values of ρ_{ab} (Equation (2)), the redistribution parameters calculated from the 1978-79 observer bias experiments, are listed in Table 6. The distance correction factors for each year $h(k)$ indicate that about 20% of passing whales are missed as a function of their distance from shore (Table 7). The cumulative proportions of the population estimated to have been observed during the census periods of around 2 mo, $\theta(k)$, indicate that between 80 and 96% of the population passed the census site during those periods (Table 7). That is, between 4 and 20% of the population passed on days before the initiation and after the termination of the annual counting efforts.

TABLE 4.—Analysis of variance for distances of sightings from shore from the 1979-80 aerial transects, with side of plane, period (morning, afternoon), and observer (Reilly, Wolman) as factors. None significant at $\alpha = 0.05$.

Source of variation	Sum of squares	df	Mean square	F
Main effects	0.385	3	0.128	0.253
side	0.062	1	0.062	0.122
observer	0.116	1	0.116	0.228
period	0.314	1	0.314	0.618
2-way interactions	1.131	3	0.377	0.743
side × obs	0.586	1	0.586	1.154
side × per	0.018	1	0.018	0.035
obs × per	0.621	1	0.621	1.224
Explained	1.516	6	0.253	0.498
Residual	124.792	246	0.507	
Total	126.308	252	0.501	

TABLE 5.—Numbers of whales observed within each of seven distance intervals from shore in aerial transects during 1978-79 and 79-80 with a χ^2 test of differences for pooling. $\chi^2 = 5.585 < \chi^2_{6, 0.25}$

Interval	Distance (mi)	1978-79 no. observed	1979-80 no. observed	Pooled (%)
1	0-0.25	14	11	2.91
2	0.26-0.5	36	33	8.02
3	0.6-0.75	41	42	9.65
4	0.76-1.0	74	88	18.34
5	1.1-1.5	148	167	36.63
6	1.6-2.0	74	61	15.69
7	2.1+	29	42	8.26
Total		416	444	

Population Estimates and Variances

The population size estimate from the 1979-80 census is 17,577, with a standard error of 2,364. Table 8 gives revised population estimates for each of the 13 yr using Equation (11), along with raw counts, variances (calculated as outlined in Appendix 2), and 95% confidence intervals (C.I.).

TABLE 6.—Values of the redistribution parameters, ρ_{ab}, and their variances.

Parameter	Value	Variance
$\rho 11$	0.6647	0.001288
$\rho 12$	0.3353	0.001280
$\rho 13$	0	0
$\rho 21$	0.2367	0.000602
$\rho 22$	0.7567	0.000614
$\rho 23$	0.0067	0.000002
$\rho 31$	0.0282	0.000386
$\rho 32$	0.8451	0.001844
$\rho 33$	0.1267	0.001558

TABLE 7.—Values of the sighting function $h(k)$, its variance, θ, the cumulative proportion predicted to have passed during the census period, and the variances of θ, for each of 13 annual gray whale censuses.

Year	$h(k)$	Var $h(k)$	θ_k	Var θ_k
1967-68	1.212	0.00958	0.8004	0.00434
1968-69	1.219	0.01143	0.9398	0.00094
1969-70	1.218	0.01076	0.9546	0.00069
1970-71	1.214	0.00889	0.9660	0.00052
1971-72	1.215	0.00619	0.8774	0.00207
1972-73	1.212	0.00857	0.9546	0.00069
1973-74	1.213	0.00848	0.9208	0.00128
1974-75	1.207	0.00642	0.9451	0.00085
1975-76	1.217	0.01112	0.9134	0.00141
1976-77	1.218	0.01170	0.9340	0.00104
1977-78	1.218	0.01607	0.9276	0.00116
1978-79	1.213	0.00659	0.9451	0.00085
1979-80	1.217	0.00929	0.9340	0.00104

TABLE 8.—Raw counts, final population estimates, their variances, standard deviations, and 95% confidence intervals for each of 13 annual grey whale censuses.

Year	Raw count	Population estimate	Variance (derived)	SD	95% confidence limits
1967-68	3,077	13,095	1,628,883	1,276	(10,593, 15,597)
1968-69	3,265	11,954	2,388,470	1,545	(8,925, 14,983)
1969-70	3,399	12,408	2,622,599	1,619	(9,234, 15,582)
1970-71	3,264	11,177	1,050,782	1,625	(9,168, 13,186)
1971-72	2,667	10,414	842,864	918	(8,615, 12,213)
1972-73	3,684	14,534	1,817,229	1,348	(11,892, 17,176)
1973-74	3,889	14,676	2,426,376	1,558	(11,623, 17,729)
1974-75	3,836	13,110	1,864,729	1,366	(10,434, 15,786)
1975-76	4,295	15,919	3,545,588	1,803	(12,228, 19,610)
1976-77	4,720	16,621	3,233,889	1,798	(13,096, 20,146)
1977-78	3,717	14,811	5,163,965	2,272	(10,357, 19,265)
1978-79	3,927	13,676	1,270,429	1,127	(11,467, 15,885)
1979-80	4,924	17,577	5,558,979	2,364	(11,943, 22,211)

Table 9 lists the mean of five subsample population estimates for each year, and the alternate variances (S_R^2) estimated from these, as well as statistics comparing variances from both methods. In 5 of the 13 yr, the variances from different methods are not equal, with the subsample estimates being generally larger. In all cases, however, the estimates are of the same general order of magnitude.

TABLE 9.—Mean estimates from five 2-h/d subsamples of each year's data, with variance (from the mean). These variances are compared with those derived for each year independently (col. 4) by χ^2 test.

Year	Mean estimate ($n = 5$)	Variance (from mean)	Variance (derived, Table 8)	χ^2
1967-68	12,301	2,326,235	1,628,883	5.7129
1968-69	11,336	474,113	2,388,470	[1]0.7940
1969-70	12,226	4,183,815	2,622,599	6.3011
1970-71	11,567	5,595,042	1,050,782	[1]21.2985
1971-72	9,745	956,377	842,864	4.5307
1972-73	15,532	9,522,245	1,817,229	[1]20.9600
1973-74	14,992	5,050,008	2,426,376	8.3252
1974-75	13,641	1,858,617	1,864,729	3.9869
1975-76	15,001	10,096,117	3,545,588	[1]11.3901
1976-77	15,833	920,392	3,233,889	1.1384
1977-78	13,588	515,923	5,163,965	[1]0.3996
1978-79	13,557	1,737,235	1,270,420	5.4698
1979-80	17,337	8,668,263	5,558,979	6.2373

[1] Significant at $\alpha = 0.05$.

Changes in Population Size, 1967-68 to 1979-80

There was a significant, positive rate of change in gray whale population size of 2.5%/yr during the 13 yr observed. The annual estimates are plotted, along with 95% C.I., in Figure 8. The unweighted simple linear model results are

$$N_t = 11{,}502.29 + 390.3 \cdot t. \qquad (16)$$

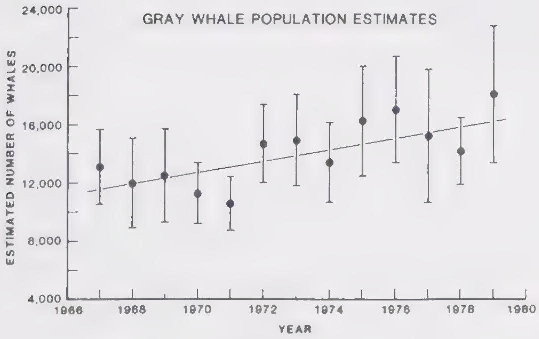

FIGURE 8.—Population estimates for the California stock of gray whales for 13 yr (1967-68 to 1979-80) with 95% confidence intervals. Fitted line is from exponential regression weighted by variances.

The coefficient of determination is 0.516, the slope is significant ($t = 3.427 > t_{11,\,0.05}$), and the 1980 population level estimate from this model is 16,186, with 95% C.I. (14,608, 17,763). The weighted $\log_e$ model results are

$$\ln N_t = 9.3313 + 0.02513 \cdot t. \qquad (17)$$

The retransformed intercept is 11,285 for the 1967 population level. The slope is also significant ($t = 2.61 > t_{11,\,0.05}$), and is an estimate of the net annual rate of increase. Expressed as a percentage, $r = 2.513$ with a standard error of 0.964. The estimated 1980 population level from this model is 15,647 with 95% C.I. (13,450, 18,201).

DISCUSSION

Five areas of investigation were mentioned at the beginning of this paper as necessary to extrapolate confidently from counts of whales passing during daylight hours to estimates of total population size. We have addressed four of these quantitatively: 1) Animals missed as a function of their distance from shore, 2) animals missed due to poor visibility conditions, 3) miscounting of the number per pod, and 4) whales passing before and after the census period. The fifth area, night travel rates (and extrapolation of daylight counts to cover these), has not been adequately addressed to date by direct observation. Our last 2-yr data show a lower count for 0700-0800 h. The low value for this hour can be interpreted in two ways: The counts may be reduced due to limited visibility during the first half of this hour before the sun is up over the coastal mountains, or the animals are in fact increasing their rate of travel as the sun rises, having slowed down at night. As discussed previously (Reilly et al. 1980), the small amount of direct evidence that does exist on night travel rates, from Cummings et al. (1968) and Rugh and Braham (1979), supports the concept of a constant 24-h rate. Lacking conclusive data on this, and for consistency, we have treated the abundance estimation for these last years in the same manner as the earlier years. That is, an hourly mean rate calculated for the 10 sampled hours is used to extrapolate over the 14 h of darkness each day. If in fact the rate is slower at night, then our estimates are biased upward by an unknown proportion. For example, if the whales slow down at night to about one-half of the daytime rate of travel, our estimate from 1979-80 would be reduced from 17,577 to 12,450. Estimates from the other 12 censuses would be similarly reduced. If the rate is indeed constant, and the depressed 0700-0800 h rates for the last two censuses are a result of limited light, then our estimates for these 2 yr are biased downward, but only by a small amount.

Because the night rate is the single largest extrapolation of the estimation procedure, more direct evidence on this would be highly desirable. Perhaps radiotelemetric studies in progress by Mate and Harvey (1979)[5] will help to clear up remaining ambiguity on this point.

The mean estimated group size increased with increasing distance from shore. This prompts two varying interpretations: This result may be an accurate depiction of whale behavior, or it may be an indication of greater sightability of larger groups farther offshore. The correction used here for whales missed offshore is based upon the assumption of equal sightability of groups, independent of group size within 1.5 mi (2.4 km), during periods of unhampered visibility. If the distribution of group sizes is in fact uniform with respect to shore, and small groups are missed near the outside of the 1.5-mi (2.4 km) zone, our population estimates would be biased downward.

Even after correction for varying amounts of poor visibility conditions and proportions of the population missed offshore, there is a considerable amount of year-to-year variation within the significant increase noted here. This may be due to further effects of visibility conditions or to unaccounted variation between counters. It also may be due, in part, to varying proportions of the population overwintering north of the Monterey area during different years. An investigation into the possible relationships of the changes in migratory timing to seasonal environmental events in the Arctic Ocean and North Pacific is in progress and may help clarify this problem.

The annual estimates presented here are slightly higher than those reported earlier (Reilly et al. 1980), especially for years with many days of poor visibility, primarily due to correction for this factor. The variances presented are also of a slightly greater magnitude than those previously reported. These are probably a more realistic representation of the variation inherent in the estimates, because they now include consideration of variation from both the effect of visibility conditions, and the inconsistency of estimating distances to passing whales. The general magnitude of the derived variances was independently corroborated by the subsampling exercise.

Regarding the current population level, we have produced three estimates: 17,577 from the latest census, 16,186 extrapolated from a simple linear model of increase, and 15,647 extrapolated from the weighted log model of increase. The 95% confidence intervals of all three overlap the point estimates. Given the range of extrapolations employed, the most conservative route is to choose the lowest, 15,647, as the "best" estimate of current population size.

A statistically significant increase in population level of about 2.5%/annum was calculated from these census results. If one also considers the annual harvest of about 164 whales by the Soviet subsistence fishery near the Chukotski Peninsula (Ivashin and Mineev 1978; International Whaling Commission 1979), the total net annual rate of production was probably near 3.75% for the past 13 yr. To our knowledge, this is the first empirical substantiation of a net increase in size by a whale population which was under exploitation.

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APPENDIX 1.—NOTATION

$\hat{n}$ = estimate of the number of whales in a passing group.

m_a = number of whales estimated to be within interval a during the regular censuses.

$\hat{m}_b$ = number of whales classified into interval b after restructuring by Equation (2).

b_n = mean bias for estimates of the number of whales in pods of n individuals.

ρ_{ab} = the proportion of the whales estimated to pass within offshore distance interval a which are actually passing within interval b.

k = the year of the census, with the 1967-68 census scaled as year 1.

$h(k)$ = offshore distance distribution correction factor for year k.

C_s = cumulative proportion of whales sighted between the shore and 1.5 mi (2.4 km) during the regular census.

C_p = cumulative proportion of the population predicted to have passed between the shore and 1.5 mi (2.4 km), by aerial transect verification.

$\hat{n}_j$ = estimate of the total number of whales passing the census site during day j, from actual counts, or from the gamma distribution, depending upon the visibility conditions.

$\Sigma\hat{n}_j$ = sum of the daily estimates.

t_j = number of hours during which a watch was conducted on day j.

$\hat{p}_j$ = the relative proportion of the population estimated to have passed the station on day j, from direct observation.

$\hat{P}_j$ = the relative proportion of the population expected to have passed the station on day j, from the gamma model.

$\hat{\theta}_j$ = the cumulative proportion of the population expected to have passed the station up to and including day j, less the proportion which passed prior to the first census day.

α = scale parameter of the gamma distribution.

β = shape parameter of the gamma distribution.

a,b = intervals of distance from shore.

N = total number of whales in the population.

$\hat{N}_j$ = estimate of the total number of whales in the population from data cumulative to day j.

$\hat{N}_k$ = estimate of population total for year k, using data cumulative to the last day of the census.

S_0^2 = variance of the estimate of the population total derived from the components of the estimation model (Equation (11)) by the Delta Method (see Appendix 2).

S_R^2 = variance of the estimate of the population total from data subsamples.

APPENDIX 2.—VARIANCE ESTIMATION

For $\hat{n}_j = (\Sigma E[n]/t_j) \cdot 24$:

$$\text{var}\{E[n]\} = \begin{cases} 0.464 ; n = 1 \\ 0.000 ; n = 2,3 \\ 0.612 ; n \geq 4 \end{cases} \text{ from Reilly et al. (1980).}$$

$\text{var}(\hat{n}_j) = (24/t_j)^2 \cdot \{\Sigma \text{var } E[n]\}$, by the Delta Method (Seber 1973).

For $n_j = (\Sigma \hat{n}_j) \cdot p_j$:

$\text{var}(\hat{n}_j) = (\hat{p}_j)^2 \text{ var}(\Sigma\hat{n}_j) + (\Sigma\hat{n}_j)^2 \text{ var}(\hat{p}_j)$,

where $\text{var}(\Sigma\hat{n}_j) = \Sigma \text{ var}(n_j)$ as above, assuming $\text{cov}(\hat{n}_j, \hat{n}_{j-1}) \simeq 0$, and

$\text{var}(\hat{p}_j) = (\delta p/\delta\alpha)^2 \text{var}(\beta) + (\delta p/\delta\beta)^2 \text{var}(\alpha) + 2(\delta p/\delta\beta)(\delta p/\delta\beta)$
$\times \text{ cov}(\alpha,\beta)$, by the Delta Method, and

$\text{var}(\alpha)$, $\text{var}(\beta)$, and $\text{cov}(\alpha,\beta)$ are estimated as in Greenwood and Durand (1960).

For $\hat{N}_k = (\sum_j \hat{n}_j)^2/\Sigma\hat{n}_j \cdot \theta_j) \cdot h(k)$:

$\text{var}(\hat{N}_k)$ is approximated by the Delta Method (as in $\text{var}(\hat{n}_j)$ and $\text{var}(\hat{p}_j)$), with component variances

$\text{var}(\theta) \simeq \theta(1 - \theta)/n$,

$\text{var}\{h(k)\} = (-C_p/C_s^2)^2 \text{ var}(C_p) + (1/C_p)^2 \text{ var}(C_s)$,

$var(C_p) = C_p(1 - C_p)/n$,

$\text{var}(C_s) = \text{var}(\hat{n}_b)$, in which

$\text{var}(\hat{n}_b) = b_a(\hat{n}_a/\Sigma\hat{n}_a)^2 \cdot \Sigma\text{var}(\rho_{a\,b})$, and

$\text{var}(\rho_{a\,b}) = \sum_a (\rho_{ab})(1 + \rho_{ab})/n_a$.

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EGG MORTALITY OF THE PERUVIAN ANCHOVY (*Engraulis ringens*) CAUSED BY CANNIBALISM AND PREDATION BY SARDINES (*Sardinops sagax*)*

by

H. Santander[1]
J. Alheit[2]
A.D. MacCall[3]
A. Alamo[1]

[1] Instituto del Mar del Peru, Apartado 22, Callao-Peru

[2] Programa Cooperativo Peruano-Alemán de Investigación Pesquera (PROCOPA), IMARPE, Apartado 22, Callao-Peru

[3] Southwest Fisheries Center, P.O. Box 271, La Jolla-CA. 92038, U.S.A.

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Resumen

En Agosto-Septiembre 1981, se colectaron 925 muestras de ichthyoplancton, y estómagos de 1 500 anchovetas (*Engaulis ringens*) y 578 sardinas (*Sardinops sagax sagax*); estas muestras fueron colectadas de una extensión de 600 millas a lo largo de la costa peruana entre los 6°S y 14°S. Los análisis de las muestras de plancton revelaron que los huevos de anchoveta estaban concentrados en una franga relativamente angosta, de alrededor de 9 millas de ancho, pararela a la costa y a una distancia de 8 a 17 millas de ésta. Los huevos no parecen ser transportados muy lejos de las áreas de desove. La tasa diaria de mortalidad de los huevos de anchoveta es extremadamente alta: 60% (Z = 0.91). Las anchovetas consumen más huevos en las áreas donde la densidad de huevos es alta y se alimentan menos de estos cuando la densidad de huevos es baja. El 61.1% de los estómagos de anchoveta y el 62.4% de los estómagos de sardina contenían huevos de anchoveta. El número promedio de huevos de anchoveta en los estómagos de anchoveta fue de 5.5, y en los estómagos de sardina fue de 16.4. Los huevos de edades diferentes parecen ser digeridos a ritmos diferentes. La predación de sardinas sobre huevos de anchoveta puede ser particularmente peligrosa ahora que el stock peruano de anchoveta ha alcanzado el nivel más bajo que jamás se haya registrado. Una comparación entre la anchoveta peruana y la anchoveta del norte frente a California (*E. mordax*) muestra que la contribución del canibalismo de huevos a la mortalidad total de los huevos es mayor en la anchoveta del norte.

INTRODUCTION

Predation on eggs either by cannibalism or by other species might regulate the size of fish stocks. Recently, egg cannibalism in the northern anchovy, *Engraulis mordax*, was the subject of a detailed investigation (Hunter and Kimbrell, 1980; MacCall, 1980). It was concluded that cannibalism on eggs and larvae is sufficiently intense to be a regulatory mechanism.

Egg cannibalism in the Peruvian anchovy, *E. ringens*, has been recorded several times (Rojas de Mendiola and Ochoa, 1973; Rojas de Mendiola, 1980). However, sample sizes were too small to draw firm conclusions. Furthermore, important parameters, e.g., egg mortality, batch fecundity, spawning rate, etc., were not known and, consequently, the impact of egg cannibalism could not be estimated.

In 1981, the Instituto del Mar del Perú, carried out a cruise to estimate the spawning biomass of the central and northern anchovy stock. The samples and data obtained from this cruise gave the opportunity to estimate the extent of egg cannibalism in the Peruvian anchovy and to determine the effect of predation on anchovy eggs by sardines, *Sardinops sagax sagax*. Further details on biological parameters used in this study on egg cannibalism are given in Santander et al. (in prep.) and Alheit et al. (in prep.). This investigation was a cooperative effort of IMARPE and the Peruvian-German Fisheries Research Project which was financed by the German Agency of Technical Cooperation (GTZ).

METHODS

In August/September 1981, 925 ichthyoplankton samples were collected by the R/V 'Humboldt' along the Peruvian coast from Pisco in the south to Punta Falsa in the north. Vertical hauls from 70 m. were carried out with the Calvet net. The area under investigation was divided up into three regions: Region 1, from Punta Falsa to Salaverry, Region 2, from Salaverry to Puerto Supe and Region 3, from Puerto Supe to Pisco. More details on the egg samples from the sea are given in Santander et al. (in prep.).

With a delay of one to two weeks, 50 collections of anchovies and 16 collections of sardines, each one consisting of about 30 fish, were taken in the same area by a purse-seiner. The body cavity of the fish was opened and they were preserved in 10% formalin.

Anchovy eggs were assigned to three different age phases according to their embryonic development. Phase 1 corresponds to stages 1-2 of Santander and O.S. de Castillo (1973), phase 2 corresponds to stage 3-11 and phase 3 corresponds to stage 12-18.

RESULTS

Comparison of the abundances of eggs in the sea and of eggs encountered in stomachs. Anchovy eggs occurred along the whole Peruvian coastline from the north, about midway between Punta Falsa and Pimentel, down to the south, to Tambo de Mora (Figure 1). High densities (more than 100 eggs per sample = 0.05 m^2) were recorded opposite Chicama, Salaverry, Chimbote, Huarmey, Puerto Supe, Huacho, Ancón, Callao and Tambo de Mora. The highest densities were around 1,000 eggs per sample, i.e., 20,000 eggs per m^2. The mean numbers of anchovy eggs per anchovy stomach are included in Figure 1.

There is good agreement between the positions of collections with high numbers of eggs per stomach and the high densities of anchovy eggs in the sea, particularly opposite Chicama, Salaverry, Huacho, Ancón and Callao. Only one collection out of 50 did not have any anchovy with anchovy eggs in the stomach, and this collection was taken outside of the distribution area of the anchovy eggs in the sea. The distribution of the sardine eggs along the coast was not continuous, as it was in the case of the anchovy, but rather patchy (Figure 2). Again, the correspondence of occurrence of sardine eggs in the sea with the occurrence of sardine eggs in anchovy stomachs was fairly good, apart from the northern area. However, it has to be taken into account that the stomach samples were

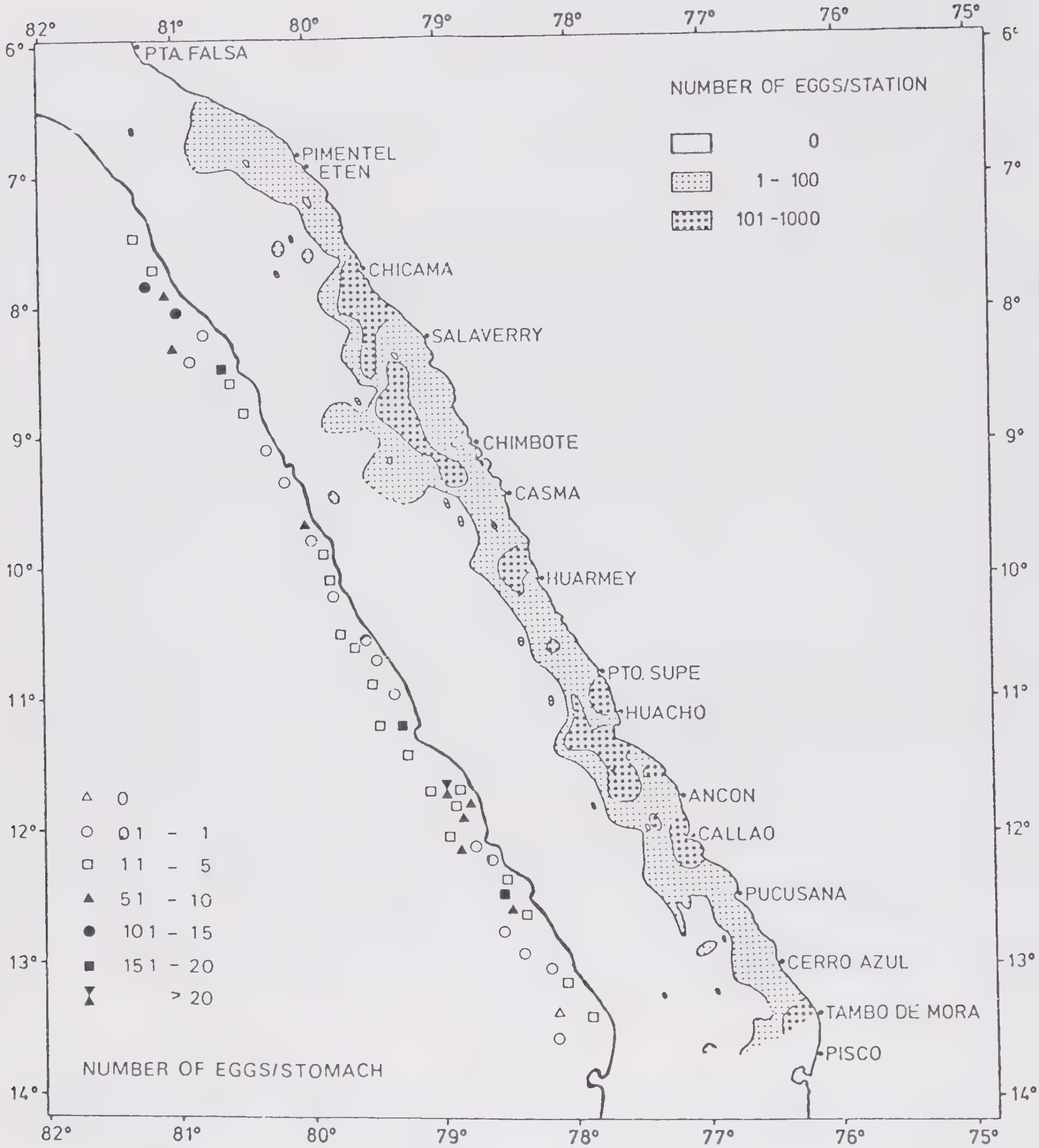

Fig. 1. Distribution and densities of anchovy eggs in the sea and in anchovy stomachs.

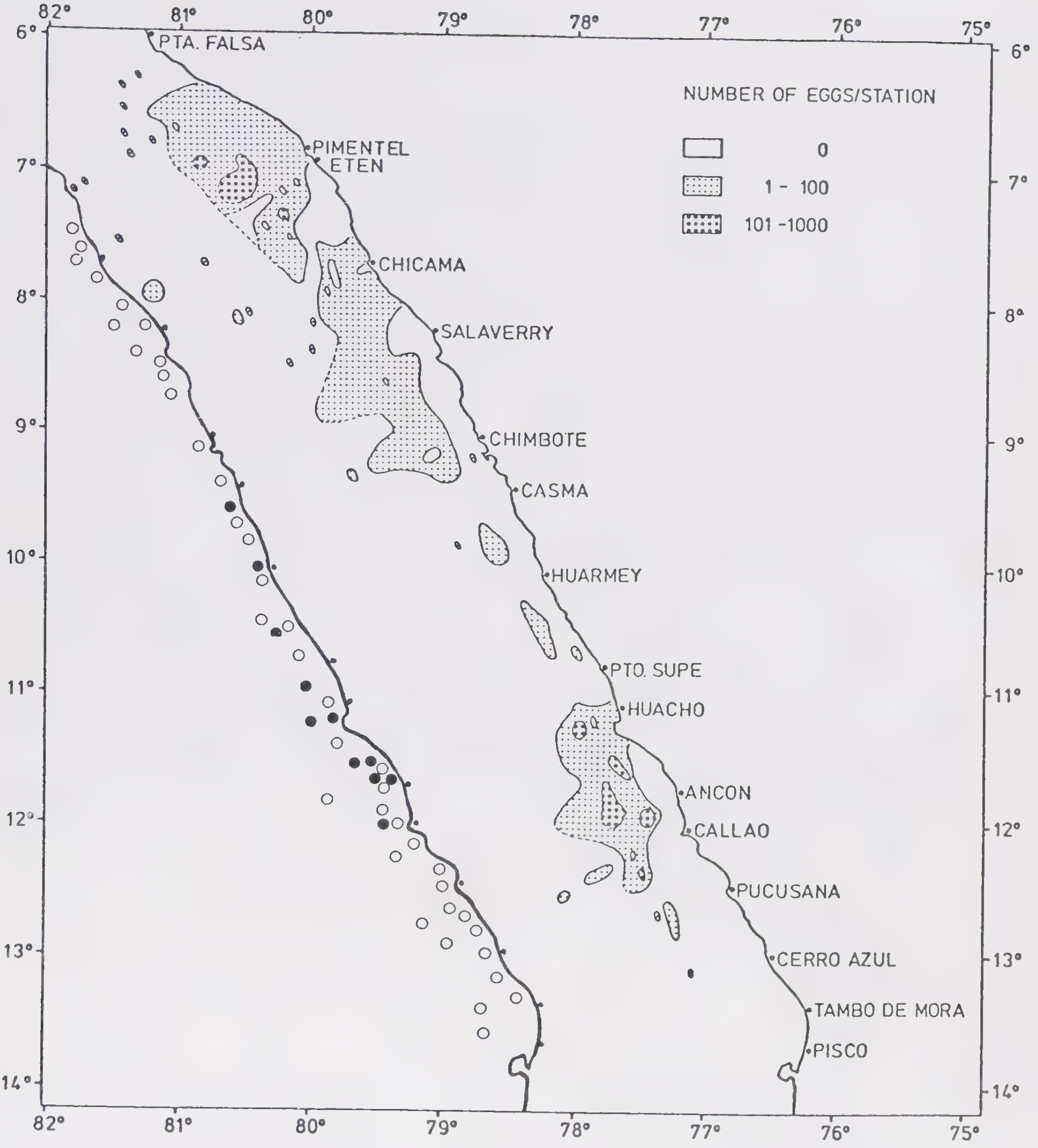

Fig. 2. Distribution of sardine eggs in the sea and in anchovy stomachs.
● = sardine eggs found in stomachs, ○ = no sardine eggs found in stomachs.

collected about one to two weeks later than the egg samples. This explains why there is not much correspondence in some areas and it demonstrates that some spawning areas are rather stable over a period of one to two weeks.

Maximum densities of anchovy egg distribution. The density peaks of anchovy eggs were encountered at different distances off the coast in the three regions (Figure 3). In Region 1, in the north, the highest densities were between 8 and 14 miles off the coast. In Region 3, in the south, the highest densities were between 11 and 17 miles off the coast. However, in the middle, in Region 2, high densities were encountered over a large area, from 8 to 29 miles off the coast. When the data of the three regions are combined, it becomes evident that the highest densities were encountered from 11 to 14 miles off the coast, and that still fairly high densities were at 8 and 17 miles. The sites of the collections with high numbers of eggs per stomach partly overlap with the sites of high densities of anchovy eggs in the sea (Figure 4). With one exception, all collections with a mean value of more than 4 eggs per stomach were collected between 5.2 and 15.6 miles off the coast. This demonstrates that the anchovies take up more eggs in areas of high egg densities and eat less eggs in areas of lower densities.

Distribution of eggs in different phases of embryonic development. From Figure 3, it was assumed that the eggs are spawned by the anchovies mainly between 8 and 17 miles off the coast and that the eggs are then transported offshore and inshore. The decrease of egg densities offshore and inshore was supposed to be caused by a dilution effect due to transportation by water movements and due to a high egg mortality. The period from the spawning of the egg to the hatching of the larva is temperature dependent and lasts in the Peruvian anchovy about 2 to 2.5 days (Santander et al., in prep.). It was expected to find young newly spawned eggs mainly in the areas of high egg densities, whereas older eggs should be encountered further inshore and, particularly, further offshore.

To study these processes, the eggs collected from the sea and from the stomachs were assigned to three phases according to the state of their embryonic development (Table 1). The distribution of the three age phases was studied separately for the three regions. In doing that, one has to be aware of the fact that the duration of the three age phases is very different. Thus, e.g. the number of eggs in phase 1 should be relatively low, because this phase lasts only about 2.4 hours at 16.5°C. In Region 1 (Figure 5) the peak of phase 1 eggs was at 17 miles off the coast. Phase 2 peaked further inshore, at 11 and 14 miles. Phase 3 had its peak at 17 miles as phase 1.

Table 1: Duration of egg phases at 16.5°C, modified after P.E. Smith (MS, 1982).

Phase	Duration (h)
1	2.4
2	28.5
3	25.3

This demonstrates that the majority of the eggs is not transported away very far from the site of their spawning. However, with increasing age of the eggs the density peaks are less pronounced and older eggs seem to be spread more evenly over the area under investigation. Similar distributional movements of eggs in different phases took place in Region 2 (Figure 6) and Region 3 (Figure 7). In all three regions, the density peaks of phase 1 and phase 3 correspond with each other exactly, whereas the peak of phase 2 is always further inshore or offshore.

For the area between 5 and 23 miles offshore, the percentages of the eggs in the three phases were calculated (Table 2). 7.2% to 19.4% of the eggs were in phase 1, 68.6% to 86.8% in phase 2 and 6.0% to 12.0% in phase 3. On average, 13.4% of the eggs were in phase 1, 78.5% in phase 2 and 8% in phase 3. The same procedure was carried out with the eggs obtained from the stomachs. However, in this case, 39% of the eggs were in phase 1, 37% in phase 2 and 23.7% in phase 3. That means, about three times as many eggs as supposed were in phase 1 and 3, whereas only about the half of that what was expected was in phase 2.

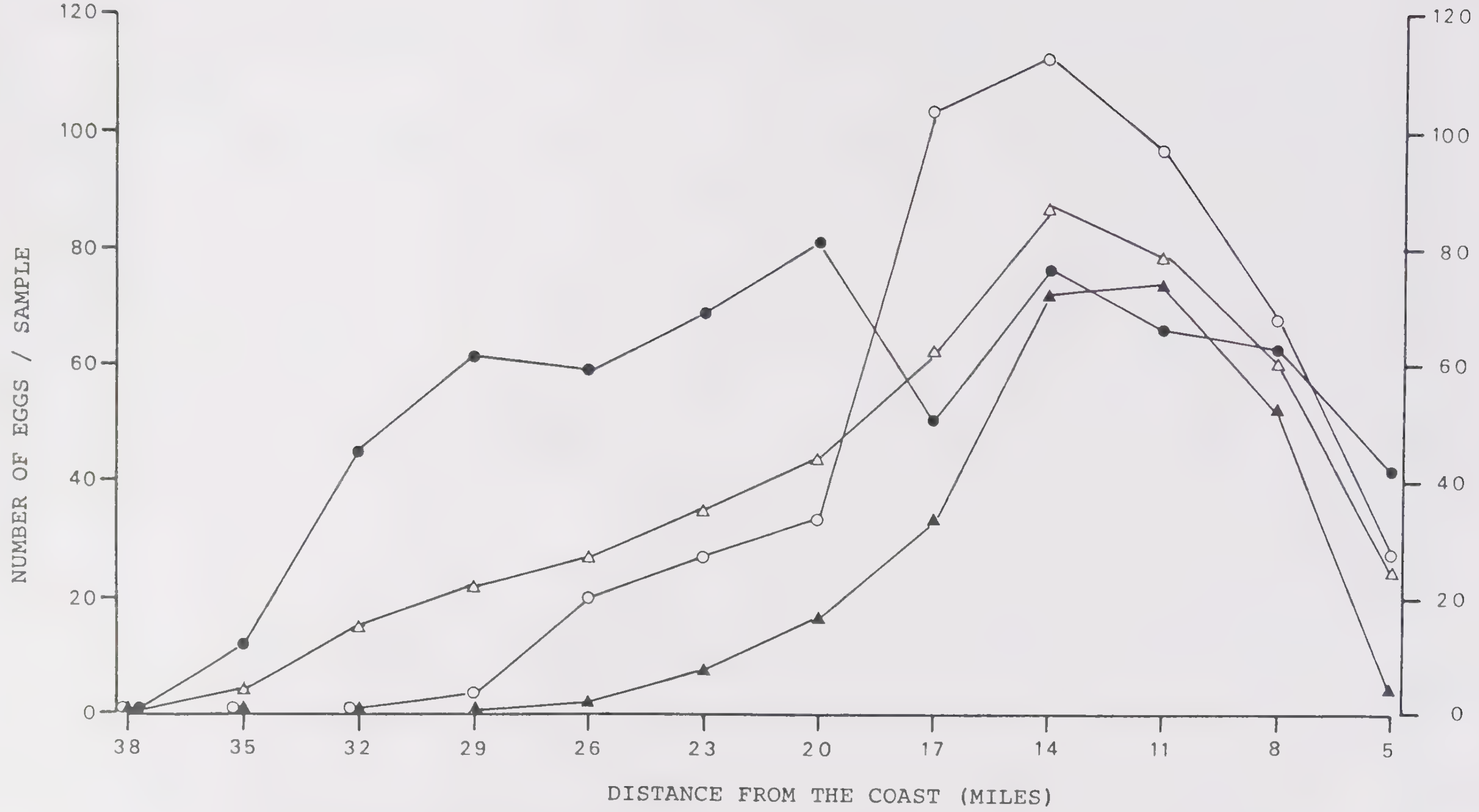

Fig. 3. Anchovy egg densities and their distance from the coast.
△ = Total area, ▲ = Region 1, ● = Region 2, ○ = Region 3.

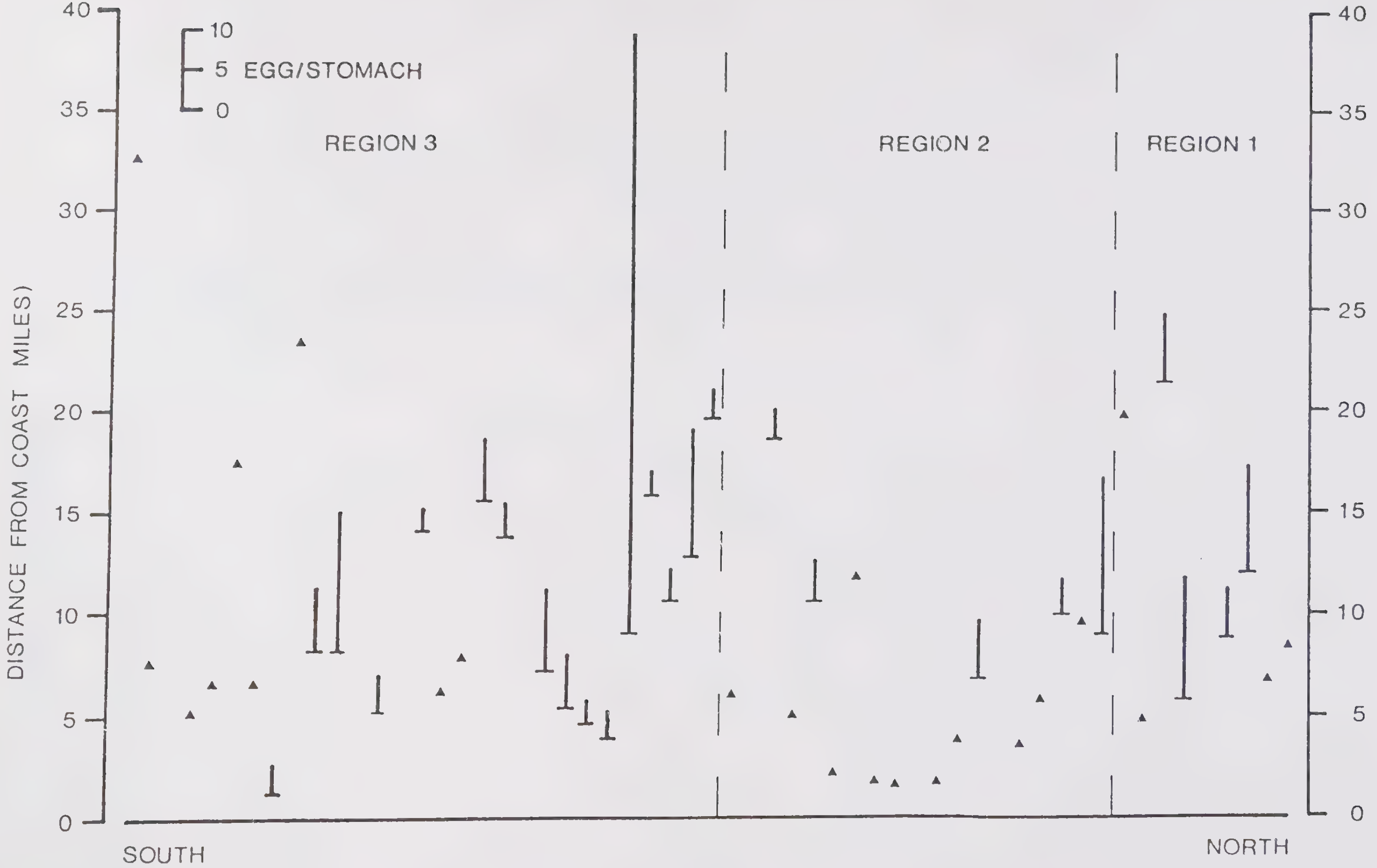

Fig. 4. Distance cf anchovy collections from coast and mean number of eggs in anchovy stomachs per collection. ⊥ = indicates in which distance from the coast the collection was taken, ▲ = less than four eggs per stomach.

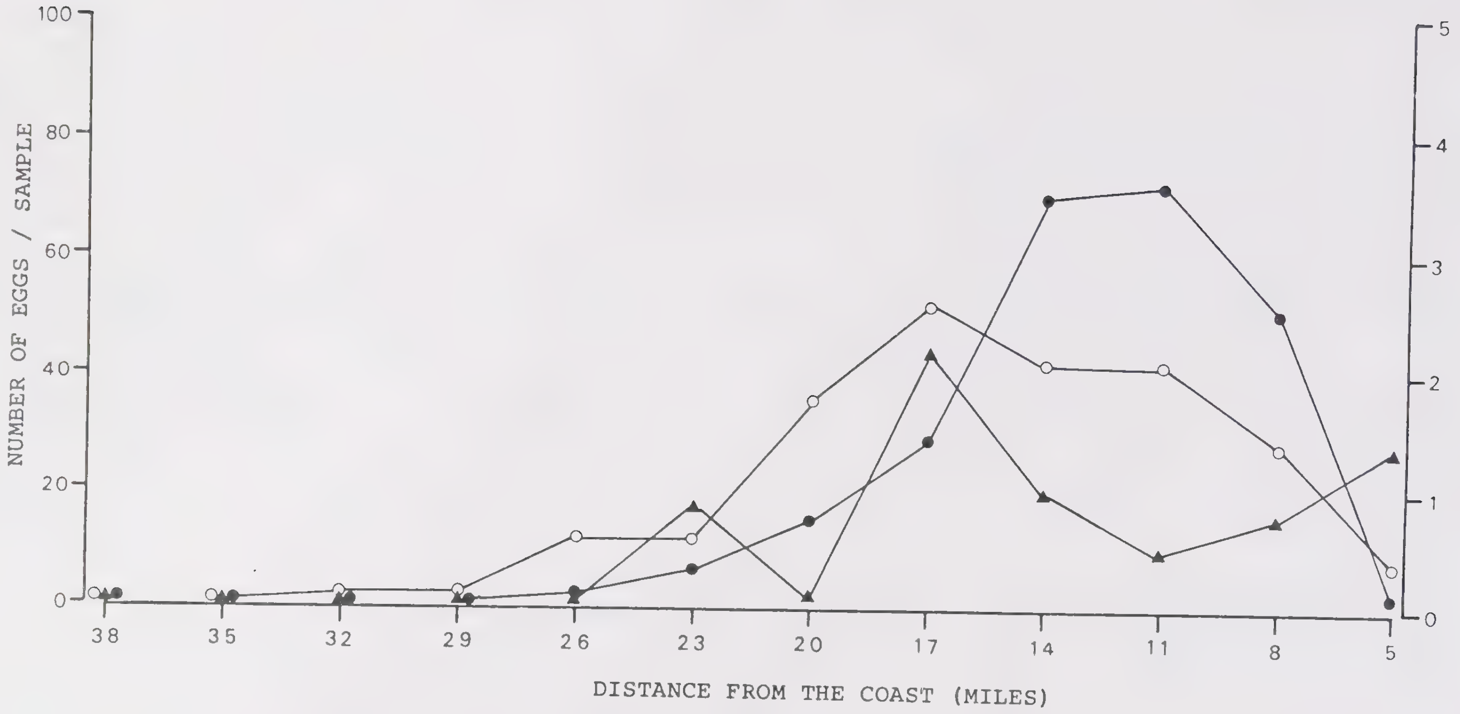

Fig. 5. Distribution of anchovy eggs, which are in different phases of embryonic development, in Region 1. ▲ = Phase 1, ● = Phase 2, ○ = Phase 3.

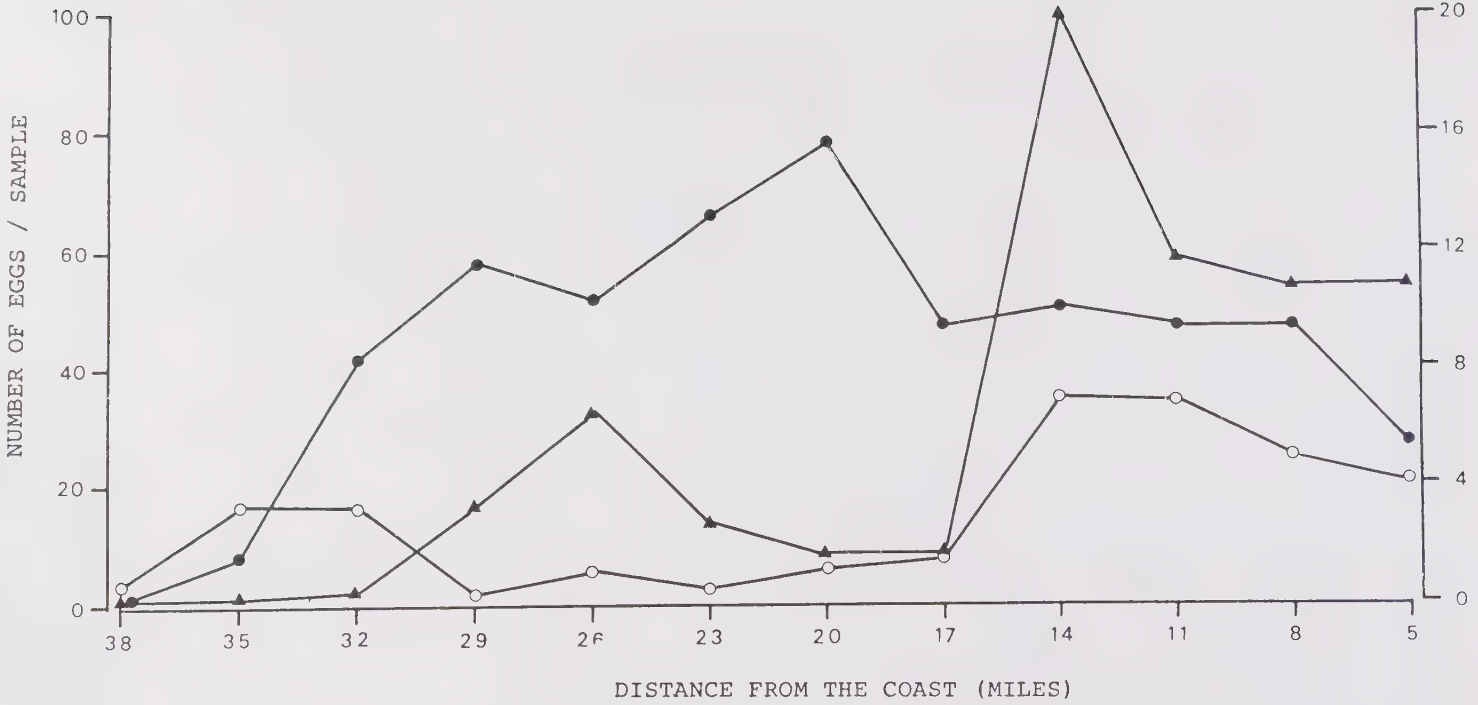

Fig. 6. Distribution of anchovy eggs, which are in different phases of embryonic development, in Region 2.

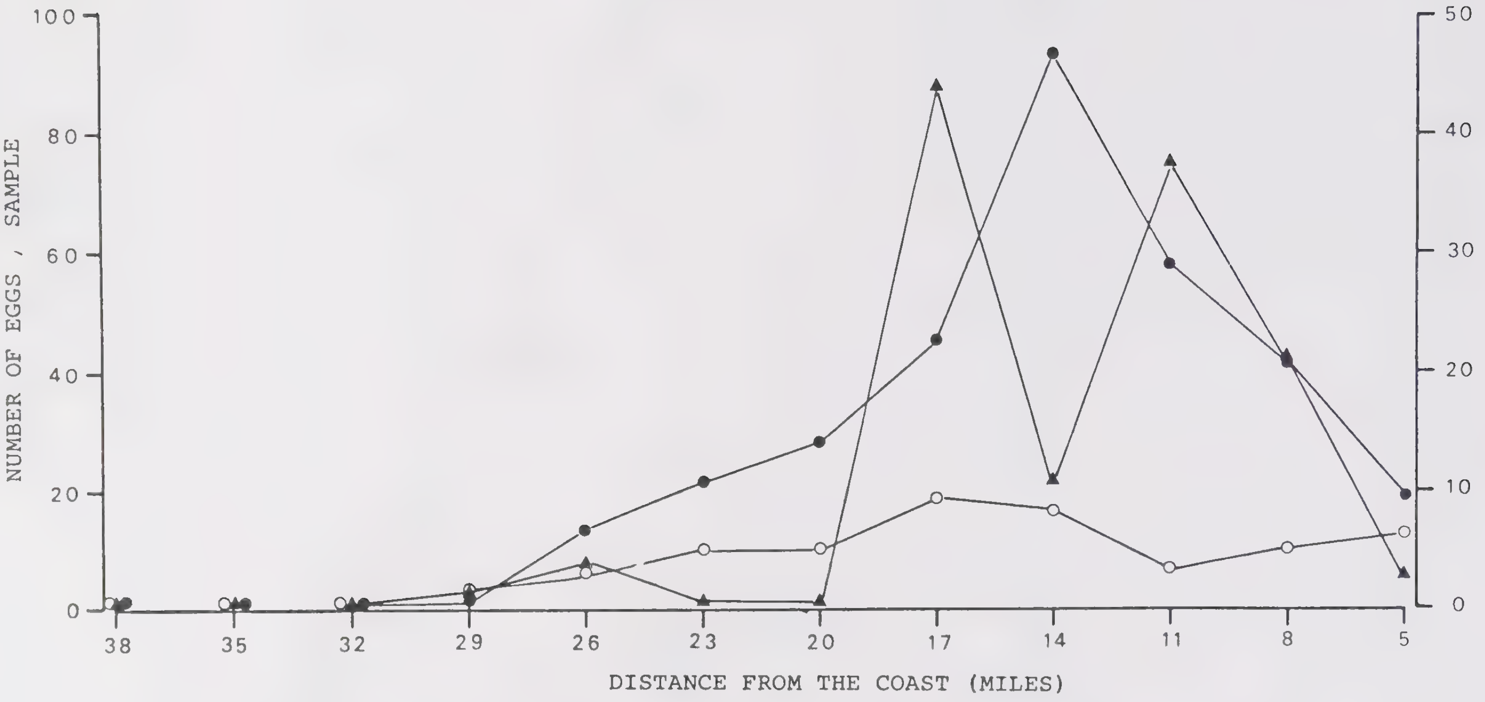

Fig. 7. Distribution of anchovy eggs, which are in different phases of embryonic development, in Region 3.

Table 2: Percentages of eggs in phase 1, 2, and 3. For the eggs collected from the sea, only the area between 5 - 23 miles offshore was considered. The total percentage of the eggs in the stomachs was calculated from all collections of stomachs.

Region	Phase 1		Phase 2		Phase 3	
	Sea	Stomach	Sea	Stomach	Sea	Stomach
Region 1	7.2	69.2	86.8	17.8	6.0	13.0
Region 2	13.7	13.6	80.2	53.3	6.1	33.1
Region 3	19.4	39.2	68.6	37.2	12.0	23.7
TOTAL	13.4	39.3	78.5	37.0	8.0	23.7

Phase 1, which lasts only about 2.4 hours at a temperature of 16.5°C, is not only overrepresented in the stomach contents, but it is encountered as well in stomachs which were collected a long time after phase 1 had disappeared from the sea. The daily spawning period starts usually at 18.00 hours at night and lasts until 02.00 hours in the morning (Santander et al., in prep.). After 05.00 hours in the morning, phase 1 eggs should not be anymore in the sea. However, phase 1 eggs were obtained from stomach samples which were taken at any time over the daily 24 hours cycle (Table 3). The percentages of phase 1 eggs in stomachs were particularly high in the morning hours and they dropped towards the late afternoon, but phase 1 eggs did not disappear totally from the stomachs at any time of day.

Table 3: Percentages of eggs in phase 1, 2, and 3. Recovered from stomachs which were collected at different times of day. Each collection had 30 anchovies.

Time of day (hours)	Number of Collections	% of eggs		
		Phase 1	Phase 2	Phase 3
07.00-10.59	11	58.5	24.5	17.0
11.00-14.59	7	53.1	32.1	14.7
15.00-18.59	9	14.8	53.9	31.3
19.00-22.59	10	30.7	38.9	30.4

Comparison of mean numbers of anchovy eggs in anchovy and sardine stomachs. A total of 1,500 anchovy stomachs from 50 collections each one containing 30 fish were analysed for numbers of anchovy eggs. Mean numbers of eggs per stomach in these 50 collections ranged from 0 to 79.4 eggs. The total mean was 5.5 anchovy eggs per anchovy stomach (Table 4). A total of 578 sardine stomachs from 16 collections each one containing on average 36 fish were analysed, too. Mean number of anchovy eggs per stomach in these 16 collections ranged from 0 to 120.0 per sardine stomach. The total mean was 16.4 anchovy eggs per sardine stomach (Table 4). According to these data, an individual sardine had about three times as many anchovy eggs in its stomach than an anchovy.

Table 4: Number of collections, total number of stomachs analysed, percent of stomachs with eggs and mean number of eggs per stomach in anchovies and sardines.

	Anchovies	Sardines
Number of collections	50	16
Total number of stomachs	1,500	578
Stomachs with anchovy eggs, %	61.1	62.4
Mean number of eggs per stomach	5.5	16.4

Calculation of percentage natural egg mortality from egg cannibalism. Hunter and Kimbrell (1980) calculated how much natural mortality is due to egg cannibalism. Their method was slightly modified by MacCall (1980) who used the catch equation to determine the coefficient of mortality due to cannibalism:

$$F_c = \frac{C_c}{E_o} \times \frac{Z}{1-e^{-Zt}}$$

Where:
C_c = daily egg consumption per gram of adults
E_o = daily egg production per gram of adults
F_c = coefficient of mortality due to cannibalism
Z = coefficient of total mortality
t = length of time eggs are subject to mortality (i.e., time from spawning to hatching).

Using Hunter and Kimbrell's (1980) method and including MacCall's (1980) modification, the percentage of mortality due to egg cannibalism was calculated for the Peruvian anchovy and compared to that of the northern anchovy (Table 5). Whereas in Peru, egg cannibalism was responsible for 10% of the total egg mortality, this value was 28% for the northern anchovy.

Table 5: Estimation of the percentage of natural egg mortality due to egg cannibalism in Peruvian and northern anchovy. The sources of the data for the Peruvian anchovy are Santander et al. (in prep.) and for the northern anchovy Hunter and Kimbrell (1980) and MacCall (1980). The variables B, C and H in the estimation for the Peruvian anchovy come from Hunter and Kimbrell (1980).

	Variable	Peruvian Anchovy	Northern Anchovy
A	Mean eggs/stomach	5.5	5.1
B	Rate of gastric evacuation	.701	.701
C	Duration of feeding (h)	24	24
D	Ration, eggs/fish	92.53	85.80
E	Mean fish weight (g)	25.8	16.8
F	Ration, eggs/grams wet weight = C_C	3.6	5.1
G	Eggs spawned/grams ovary-free female weight	581	389
H	Ratio of ovary-free weight to total female weight	.954	.954
I	Eggs spawned/grams total female weight	554	371
J	Ratio of females spawning/night	.16	.16
K	Ration of females/school	.5	.5
L	Eggs/gram school weight = E_0	44.4	29.7
M	Coefficient of natural egg mortality = Z	.91	.39
N	Length of time eggs are subject to mortality = t	2.0	2.5

DISCUSSION

At the present state of knowledge, it is difficult to explain why eggs of phase 1 and 3 are overrepresented in anchovy stomachs. Misidentification is clearly not the reason, as eggs of the three phases cannot be confused with each other. All eggs which could not be identified were labelled as 'disintegrated' and not included in the calculations. However, it might be that eggs of phase 2 are particularly vulnerable to 'disintegration' in anchovy stomachs. Furthermore, as not much is known about the vertical distribution of anchovy eggs in different stages of embryonic development, it could be argued that phase 2 eggs are in depths in which the anchovies feed less. However, that does not seem very probable.

Another puzzle is the occurrence of phase 1 eggs in fish stomachs collected in the late afternoon. The analysis of the egg samples from the field demonstrated clearly that spawning is terminated at 02.00 hours and that no spawning takes place in daytime. The only explanation is that phase 1 eggs encountered in fish stomachs collected in the late afternoon must have been fed upon a long time before the fish were collected. That means, they must have spent several hours in the fish stomachs without being affected much by digestive processes. Hunter and Kimbrell (1980) report that identifiable parts of eggs may remain in the stomachs up to 8 hours, but the contents of the eggs (embryo and yolk) are digested after 2 hours. As the content of phase 1 eggs from stomachs collected in the afternoon was not damaged, one may conclude that phase 1 eggs are particularly resistant towards digestive processes. This supports the above mentioned hypothesis of differential vulnerability to 'disintegration' of eggs in different age phases.

The data in Table 5, give the impression that egg cannibalism in anchovies plays a less important role in the Peruvian anchovy. This would be surprising as the egg densities in the Peruvian ecosystem are higher than in the Californian system (Santander *et al.*, 1982). However, it has to be considered that different methods were applied to collect the fish. Whereas, in California, the fish were caught with a trawl, in Peru, the anchovies were sampled with a purse-seiner. A purse-seine haul lasts usually 2 to 3 hours. If the fish stop feeding when the haul begins, a high number of eggs might already be digested by the time the fish are fixed in formalin. According to the gut evacuation rate determined in the laboratory by Hunter and Kimbrell (1980), the mean residence time of eggs in the stomach is only 1.4 hours. The 10% contribution of cannibalism to the total egg mortality estimated for the Peruvian anchovy (Table 5) has therefore, to be considered only as a minimum estimate.

For a long time, it has been speculated that exploited clupeoid species might be suppressed by competitors feeding on eggs and larvae (e.g. Murphy, 1977). The data on sardines predating on anchovy eggs which are presented here support this hypothesis. The mean number of anchovy eggs in sardine stomachs is more than three times higher than in anchovy stomachs (Table 4). However, it is not possible yet to estimate the consumption of anchovy eggs by sardines, as the stock size of the sardines in the spawning area of the anchovy is not known. Predation on anchovy eggs by sardines might be particularly dangerous to the central and northern Peruvian anchovy stock now, as the sardine stock seems to have been increasing over the last years (J. Valdivia, pers. comm.) whereas the anchovy stock has reached its lowest level ever recorded (Santander *et al.*, in prep.).

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COMPARISON OF EGG SAMPLE PROBABILITY DISTRIBUTIONS OF THE ANCHOVY (*Engraulis ringens*) AND SARDINE (*Sardinops sagax*) OFF PERU AND THE ANCHOVY (*Engraulis mordax*) AND THE SARDINE (*Sardinops caerulea*) OFF CALIFORNIA

by

Paul E. Smith,[1] Haydee Santander[2] and Jürgen Alheit[3]

[1]Southwest Fisheries Center
P.O. Box 271
La Jolla, CA 92038
USA

[2]Instituto del Mar del Perú
Esq. Gamarra y Gral. Valle
Apartado Postal 22
Chucuito, Callao
Perú

[3]Programa Cooperativo Peruano-Alemán de
Investigación Pesquera (PROCOPA)
Instituto del Mar del Perú
Esq. Gamarra y Gral. Valle
Apartado Postal 22
Chucuito, Callao
Perú

Resumen

Se dispone de datos de reconocimiento de ictioplancton de más de 20 años del sistema de afloramiento del Perú y de más de 30 años del sistema de afloramiento de California. Se comparan las distribuciones de probabilidad de muestras de huevos de dos especies de clupeidos de estos dos sistemas (*Engraulis ringens* y *Sardinops sagax* del Perú y *E. mordax* y *S. caerulea* de California). El análisis de las distribuciones de las muestras de huevos combinado con datos adicionales permite estudiar actividades biológicas importantes de peces pelágicos, tales como agregación, fertilización, etc. Además se puede determinar la efectividad de canibalismo directo e incidental, de la predación, y de otras causas de mortalidad a través de la distribución inicial de huevos y la dispersión subsiguiente y el transporte hacia afuera de las áreas de desove. La escala e intensidad del patrón cambian con el tiempo y pueden afectar el esfuerzo de muestreo que se requiere para estimar la producción y sobrevivencia de los huevos y pueden complicar el ajuste de las ecuaciones de mortalidad que asumen una varianza constante con términos absolutos o relativos.

INTRODUCTION

The egg sample probability distribution of the Peruvian anchovy (*Engraulis ringens*) has been used to design an egg production survey with precision estimated from existing samples by Santander, Smith, and Alheit (1982). It should be possible, with existing data, to estimate the optimum survey effort for the determination of egg production of the sardine off Peru and California and analagous multiple pelagic-spawners of other species and in other areas, given historical sample data.

It is the purpose of this paper to briefly compare historical data on egg abundance per sample for four stocks from two genera (*Engraulis* and *Sardinops*), from two habitats (Peru and California). While it is not yet possible to infer historical egg production rates from these sets of data it should now be possible to estimate the number of samples needed for a given precision in future surveys. Also the analysis of sample probability distributions may lead to new insights into the origins of patches of eggs and the fate of the spawning products as they disperse (Smith,1973) and the causes and degree of variation in the survival of the spawning products. This study was part of a cooperative project of the Southwest Fisheries Center, California, the Instituto del Mar del Peru and the "Cooperative Peruvian-German Fisheries Research Project" (PROCOPA) which is financed by the "German Agency of Technical Cooperation" (GTZ).

METHODS

Detailed accounts of sampling and sorting methods are given by Santander and S. de Castillo (1979) for the Peruvian samples and by Kramer et al. (1972) for the Californian samples. Briefly, the IMARPE samples are from a Hensen Egg Net towed vertically from 50 meters depth sampling directly under 0.3 square meters. The CalCOFI samples were towed obliquely from 140 or 210 meters. To report the values in similar units the IMARPE samples are divided by 3 and both are reported here as eggs per square meter sea surface area.

RESULTS

The number of anchovy eggs in the IMARPE samples was greater than the number of anchovy eggs in the CalCOFI samples. The number of sardine eggs in the IMARPE samples was greater than those in the CalCOFI samples. Both species of the genus *Engraulis* yielded number of eggs greater than the cohabitant of the genus *Sardinops* (Figures 1 and 2).

Part of the differences between the numbers of eggs per sample are due to the sampling technique. Some anchovy eggs are lost through the meshes of the CalCOFI net. Also the lower treshhold of egg density detected by the IMARPE net is higher (3 eggs per square meter) than that detected by the CalCOFI net (approximately 0.3 eggs per square meter). Since the bulk of the population at the egg stage is in the larger samples, it is not likely that these differences will be important.

The difference in sardine eggs per unit surface area between IMARPE samples and CalCOFI samples is of the same order of magnitude as the difference in anchovy egg sample sizes. In both cases the difference is between 4- and 16-fold. This signals a radical difference between the Peruvian and Californian habitats which directly effects both sardine and anchovy at the time of spawning and during the subsequent dispersal and mortality phase.

DISCUSSION

The most important result of this study is that for a given precision it will be necessary to take more series in the area of spawning to estimate the egg production of the stocks of *Engraulis* and *Sardinops* off Peru than off California. That this is not inherent in the different methods of sampling or different stock sizes is indicated by the stability of the egg distributions of the Californian sardine when several different samples sizes were used while the spawning biomass changed from 4 million tons to less than 10 thousand tons (Smith and Ricardson, 1977).

FIGURE 1

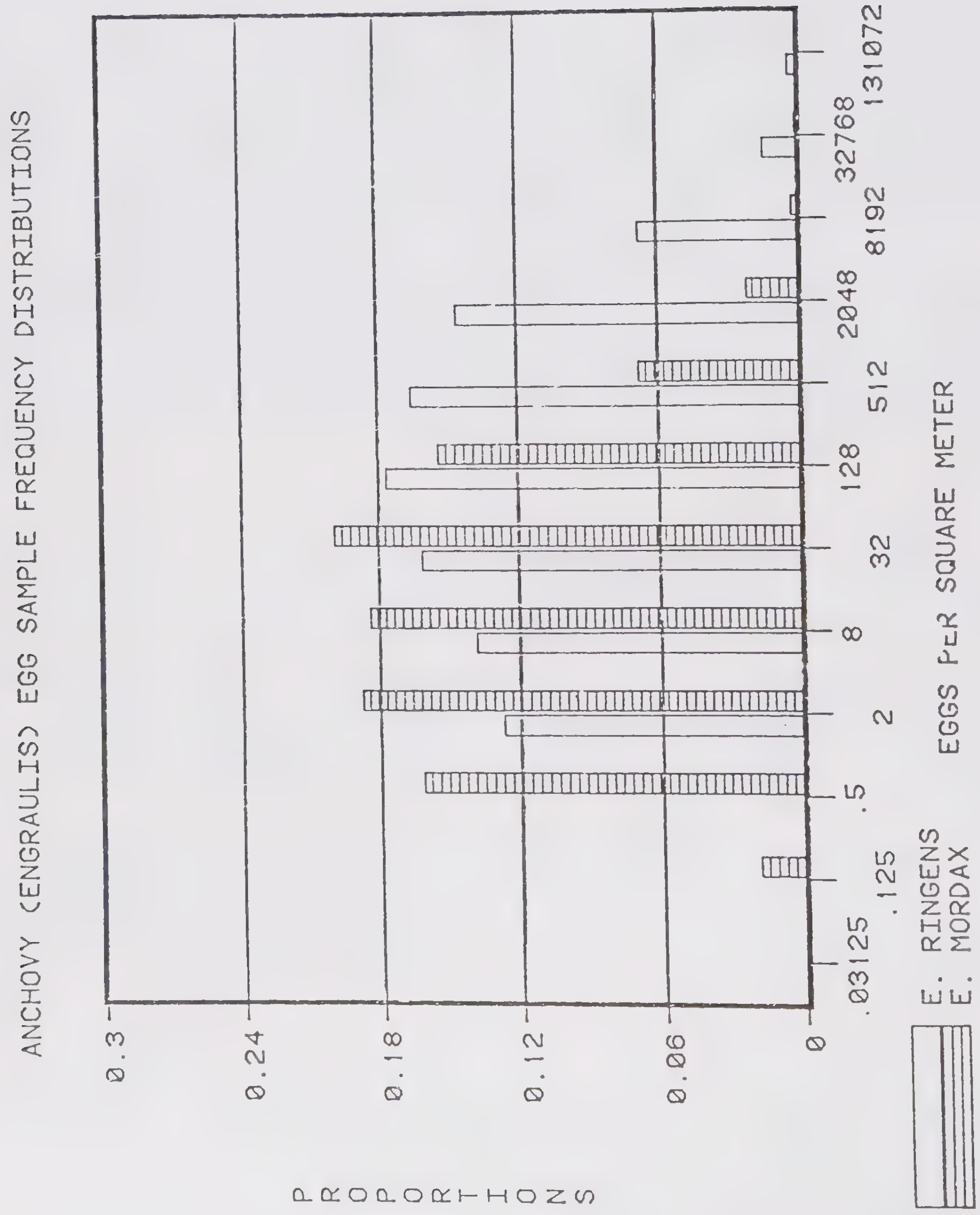
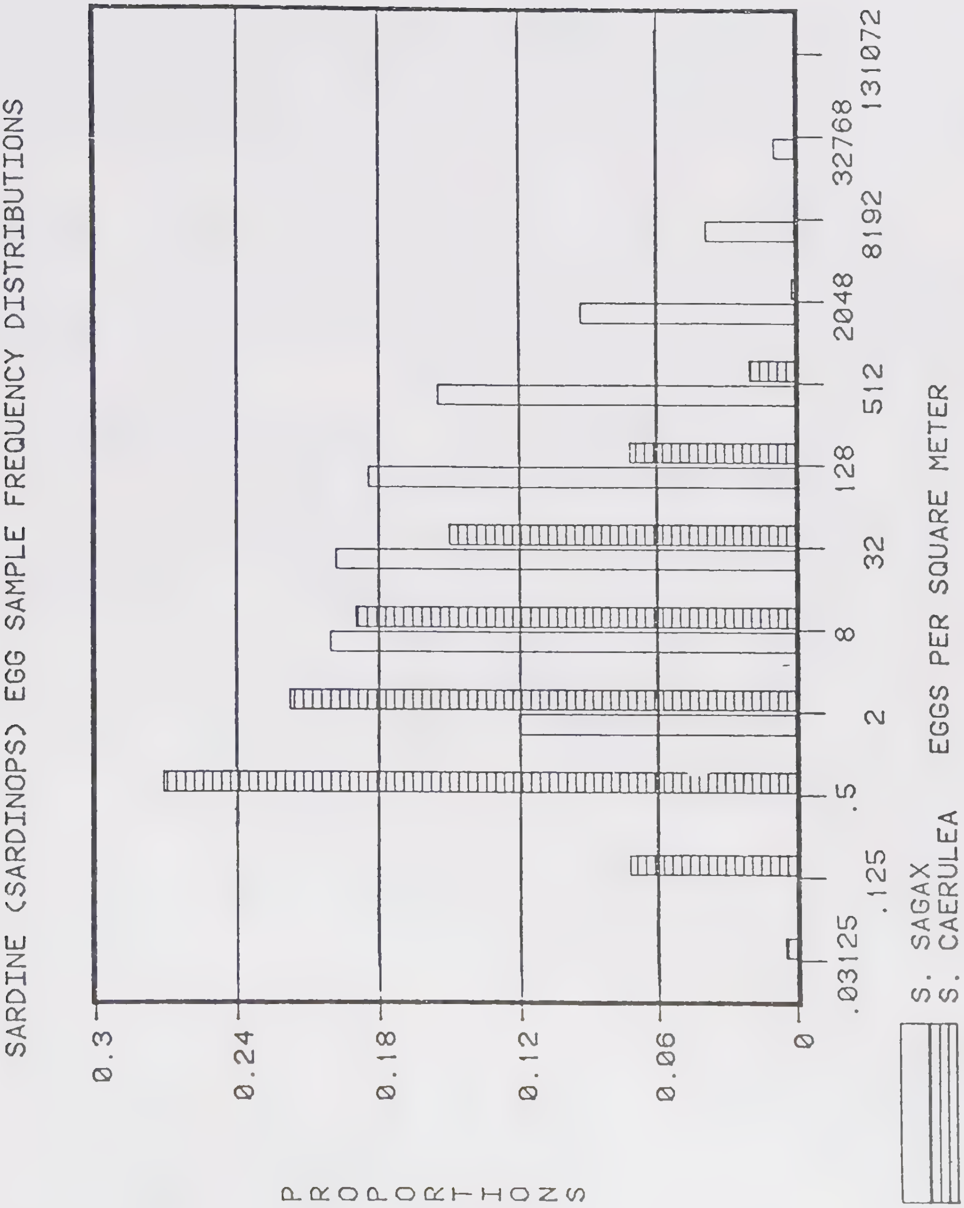

ANCHOVY (ENGRAULIS) EGG SAMPLE FREQUENCY DISTRIBUTIONS
PROPORTIONS
0.3
0.24
0.18
0.12
0.06
0
.03125
.125
.5
2
8
32
128
512
2048
8192
32768
131072
EGGS PER SQUARE METER
E. RINGENS
E. MORDAX

FIGURE 2


SARDINE (SARDINOPS) EGG SAMPLE FREQUENCY DISTRIBUTIONS
PROPORTIONS
0.3
0.24
0.18
0.12
0.06
0
.03125
.125
.5
2
8
32
128
512
2048
8192
32768
131072
EGGS PER SQUARE METER
S. SAGAX
S. CAERULEA

To explore the meaning of the egg sample distributions presented here, it is necesary to postulate a conceptual framework for the four stocks of fish which incorporates spatial distribution of mature adult fish at the time of spawning and the time distribution of the spawning process.

Spatial scale and intensity of distribution: Unfortunately the features of spatial scale and intensity are not equally well known for the four stocks examined here. The geographic distribution of all four species is well known. Also, the stock boundaries are well known in the offshore-onshore plane, but are less well known along the coast and these stock divisions may fluctuate with season and with interannual climatic conditions of changes in stock biomass (see MacCall, in prep.).

For scales of distribution below the species, and stock or subpopulation, only the beginning of perception has been reached for *Engraulis mordax*. Schools are unevenly distributed in the habitat and the aggregations of schools are called "school groups" or "shoal groups" (Fiedler, 1978). These can be characterized as 3000 schools in a 6 nautical mile (10 km) disc with 100 schools per square nautical mile. While most of the schools are small (15 m radius) most of the fish are in large schools (50 m radius). The school groups probably include all ages and sizes of fish but the schools probably consist of either "0" group or adult but not both.

Hewitt, Smith and Brown (1976) estimated that the schools contained 15 kilograms of mature fish per square meter of which some faction are ready to spawn each night. It is not known what fraction of males participate in spawning each night. The females spawn in the height of the spawning season each 6 to 8 nights (Hunter and Macewicz, 1980; Alheit et al., this volume). That the spawners for a given night segregate within the school before spawning is suggested by the odd sex ratios (3 or 4 males per female) and above average proportions of spawning females.

It is also not known how the various spawners are arrayed at the time of spawning. The quantity of sperm available probably limits the volume through which the eggs are distributed. For the purpose of this discussion we shall use the concentration of ten thousand to one hundred thousand eggs per cubic meter.

In summary, the species involved in this paper extend for one or two thousand miles of coastline in the temperate zone of the Pacific coast of North and South America and into the tropics of South America. The species are apparently subdivided into stocks or subpopulations extending a few hundred miles along the coast within tens of miles of the coastline in South America and within a few hundred miles of the coast in North America. We assume that these stocks form school groups of a few nautical miles extent and these are comprised of schools of tens of meters radius concentrated at 100 schools per nautical square mile. Within the schools in daytime, there are about 15 kilograms of fish per square meter of surface area. The night-time concentration is assumed to be less dense. Also, in the spawning season, the spawning females and their male attendants segregate early in the evening to spawn and fertilize the spawn and reaggregate with the schools before dawn.

Temporal scales of egg production: The early work on spawning frequency (Hunter and Goldberg, 1979; Alheit et al., this volume) indicates that a female of the genus *Engraulis* may spawn a hundred or so batches of eggs in her lifetime. The female may spawn a limited number of times in the first year of life and in later years may spawn 30 times per year. The spawning appears to be intensified seasonally, beginning in the winter months and persisting for some months, depending on the age, size, and condition of the female and the feeding conditions. Hunter (pers. comm.) believes that spawning rate in *Engraulis mordax* is controlled by the amount of fat stored in previous summer and the feeding conditions at the time of spawning. Hunter and Leong (1981) state that 10 to 15 batches could be spawned using the energy in stored fat and that subsequent spawnings would be derived from feeding during the spawning season. Smith and Eppley (1982) found a correlation suggestive of a link between the zooplankton abundance in the preceeding summer and the larva abundance in the spawning season. Hunter (pers. comm.) believes the pattern of atresia or resorption of oocytes prior to spawning matches this viewpoint since atresia is most common in young fish with little stored fat and with older fish late in the season of heaviest spawning.

On the daily time scale, the collective spawning interval extends from about sundown to a couple of hours after midnight with a propensity to spawn within 3 hours of midnight. It appears that individual females spawn in a very short time because the increasing incidence of samples with newly spawned eggs (fraction of samples with newly spawned eggs) and the increasing abundance of newly spawned eggs (newly spawned eggs per sample) with time are nearly parallel. If individual females spawned over an 8 hours period one would expect the incidence of newly spawned eggs to rise rapidly with the change in abundance following many hours later.

These general features appear to be similar for *Engraulis mordax* and *E. ringens*. The life span of the *Sardinops* is much longer but the number of spawnings or the maximum rate of spawning is not known for this genus. However the daily cycle of spawning is similar in *Sardinops caerulea* (Smith,1973).

Changes of spatial scale with time: At the moment of spawning, the *Engraulis* schools are at the scale of tens of meters and the scale of the egg patches of *Sardinops* and *Engraulis* are on the scale of hundreds of meters (Smith,1973; Smith and Hewitt MS) and the yolk sac larvae patches are on the scale of a few thousand meters (Hewitt,1982). In a period of five days after spawning turbulent diffusion has spread the newly spawned eggs, covering at most a few tenths of one percent of the sea surface in the spawning area to covering nearly 70% of the sea surface at hatching time.

There may be different explanations for the greater intensity of *Sardinops* and *Engraulis* egg distribution off Peru as compared to California and the differences between the *Engraulis* in both hemispheres and the *Sardinops* in both hemispheres. To consider these, we must establish some useful categories of causes for differences in the scale and intensity of patches of eggs. One category of difference can be termed "demographic". That is if the age distribution of the females is older the stock will be made up of larger fishes and for the two genera the size distribution of *Sardinops* females will be larger than *Engraulis* females. Another category of difference can be labeled "behavioral". That is if the individual females behave in such a way as to distribute their spawn in smaller, more compact patches this would retard subsequent dispersal rates relative to females which disperse their spawn in larger, more diffuse patches. Another category of difference causing changes in distribution of sample sizes of eggs could be labeled "environmental". That is the subsequent mixing of the spawning products or the pattern of mortality could in time impose a different sample frequency distribution. We shall discuss these categories in more detail.

Demographic factors affecting the number of eggs per sample: The relationships between fish weight and eggs per gram of fish weight are not completely known for *Engraulis mordax, Engraulis ringens, Sardinops caerulea,* and *Sardinops sagax*. For *Engraulis mordax,* the relationship is apparently linear (Picquelle and Hewitt,1982; Alheit et al.,in prep.) for the period 1980 through 1982 for the central subpopulation. Neither *E. mordax* nor *E. ringens* have been examined with regard to age-specific fecundity as distinguished from size-specific fecundity. Even though age and weight are related, the differences between weight at age and the ranges of weights and ages could explain the differences apparent in the linearity of the fecundity with weight. It is not known how this would affect the distribution of eggs in the sea. If the older or larger females were capable of spawning more eggs into a column of water there could be persistent changes in the egg sample distribution. However, it appears that the *Sardinops* places fewer eggs in a column of water even though the female of the genus *Sardinops* is larger than the female of the genus *Engraulis*.

Another demographic feature is age and size at first maturity. Females of genus *Engraulis* appear to begin maturation in the first year of life while the females of the genus *Sardinops* mature somewhat later and at a larger size. Within *Engraulis mordax* females it is characteristic for the "0" group females to begin spawning later in the season and stop sooner than females of the older cohorts. If there were similar maturational features in the genus *Sardinops,* this could lead to both inter-specific and inter-generic differences by some influence on the number of eggs spawned in a column of water according to size. In this case, smaller movements of smaller females would tend to increase the number of eggs per unit surface area. While this would explain the inter-generic differences it is contrary to the interspecific differences in *E. mordax* with an average female weight of 16 grams while *E. ringens* with higher numbers of eggs per unit surface area had female weights in the range of 25 grams.

In summary, it is not clear how demographic features could by themselves explain the differences in eggs per unit surface area. It seems more likely that demographic features would be coupled with behavioral and environmental factors to change the distribution of spawn.

Behavioural factors affecting the number of eggs per sample: On the geographic scale, if the adults of the species aggregate on a specific spawning site this would tend to increase the number of eggs per unit area within the spawning area. It is known that *Sardinops caerulea* migrated to a spawning site hundreds of miles from the feeding zone. To what degree the *Engraulis* species do this is not known but the *Engraulis ringens* spawning zone appears to be much more restricted in distance from shore than that for *Engraulis mordax*. Thus one source to be considered for the differences in the number of eggs per sample is the degree to which the spawners aggregate for spawning. This increases the chance that areas with new spawn would overlap other spawning sites from previous days and thus the number of eggs per unit surface area would be higher. If this were the main cause the order of concentration at spawning time would be *Engraulis ringens*, *Engraulis mordax*, *Sardinops sagax* and *Sardinops caerulea*. This behavioural factor could interact with population demography if the older and larger females were more capable of assembling denser spawning aggregations.

Another behavioral factor could apply at the individual spawning fish scale. For example, if one species, say an *Engraulis* in this case, were to continually turn and circle while spawning and *Sardinops* were to undertake long spawning runs in a straight line, this could affect the initial concentration of eggs and the subsequent dispersal rate. If linear spawning runs were the usual, this would also interact with the demographic factors by faster swimming rates.

Environmental factors affecting the number of eggs per sample: Temperature, turbulence, predation and production are environmental factors affecting the number of eggs per sample. Temperature influences the developmental rate of the eggs (Table 1) and thus influences the probability that the eggs from two different spawning concentrations would be found in a single sample. For example the largest sample of 1300 samples of *Sardinops caerulea* eggs taken between 1951 and 1959 contained two ages of eggs two days apart in age (Smith,1973). The probability of this kind of event would increase in colder water. The duration of the egg stage at 13 degrees Celsius is about four days for *Sardinops* and *Engraulis* and two days at 18 degrees. This does not appear to be the case for the stocks under investigation. The IMARPE samples are from warmer temperature than the CalCOFI samples.

Table 1

TEMPERATURE AND INCUBATION TIME FOR
ENGRAULIS MORDAX AND *SARDINOPS CAERULEA*
(ZWEIFEL AND LASKER, 1976)

INCUBATION TEMPERATURE	*ENGRAULIS MORDAX*	*SARDINOPS CAERULEA*
11		5.8 days
11.1	4.7 days	
12		4.8
12.5	4.1	
13		3.9
13.8	3.3	
14		3.3
15		2.8
15.2	2.6	
16		2.5
16.6	2.3	
17		2.2
18	2.0	2.0
19		1.8
19.4	1.7	
20		1.6
20.8	1.5	
21		1.4

Turbulent diffusion could have a major effect on the number of eggs per sample. It appears that both *Engraulis* species and *Sardinops* select areas and seasons which minimize turbulent diffusion and offshore transport (Bakun and Parrish, 1982; Husby and Nelson, 1982) off the Pacific coastline of both North and South America. It seems likely that the differences in egg sample numbers could be controlled by the rate of the turbulent diffusion or by a combination of higher initial concentrations of eggs interacting with the lower rate of turbulent diffusion which this would imply.

The effect of predation on the numbers of eggs in each sample would be to change the probability of more than one day's spawning being taken at the same time. It would also be important to know if predation interacted with behavioral features of the predators including cannibals. For example if the predation were merely incidental to feeding on other food particles there would be a proportional drop in all ages of eggs in numbers per unit area. If there were directed predation on the densest concentrations of eggs there would disproportionately higher losses in the earlier ages at the highest concentrations. This could also have an effect on the differences between *Engraulis* and *Sardinops* eggs as the latter are much larger and may be filtered by more predators. The difference in effects would rest on the relative concentrations per unit volume even though the effect would eventually be expressed in numbers of eggs per unit sea surface. The relative visibility of the *Engraulis* and *Sardinops* eggs would be important for visual predators. The differences between the stocks in different hemispheres would also depend on the abundance and effectiveness of the predators found in those waters in the spawning season. Production may influence the numbers of eggs per sample. One way in which food production could control the numbers of eggs per sample is by increasing the frequency of spawning. So far the applications of the SWFC Egg Production Method have found the frequency of spawning off California to be 14.5% in April of 1980, 10.6% in February of 1981, 12,5% in April of 1981, and 12.0% in February of 1982. Off Peru in August-September of 1981, the percent spawning was 16%. This translates to a group average of mature females spawning each 6 days respectively. Spawning at high frequency would influence the chance of two spawning patches overlapping which would increase the range of egg numbers and increase the chances of sampling the origin of an egg patch which would increase the frequency of sampling large numbers of eggs less than the maximum.

Another mechanism for production to influence the number of eggs in a sample is by controlling the feeding behavior of the reproducing stock. For example if the stock were distributed so as not to depress the number of herbivores, the feeding behavior of *Engraulis* and *Sardinops* would be by biting-diminishing the incidence of cannibalism by inadvertant filtering. If production were lower and the growth of the herbivore populations were depressed by the fish, then the incidence of filter feeding and incidental cannibalism would increase, diminishing the numbers of eggs per sample.

Another factor controlled by production would be if the mean motion of that portion of a school which is spawning were reduced in favorable feeding areas and increased in less favorable feeding areas. For example a daytime school may contain 15,000 grams of adult fish per square meter of sea surface area over the school. With no net motion nor spreading of the school at night, there would be 7,500 grams of females and about 1000 grams of spawning females per square meter of sea surface area. With a batch fecundity of 500 eggs per gram, there would be 500,000 eggs per square meter, a number higher than yet observed for any of the four stocks considered here. If the feeding activities carried the school 250 meters during the half-hour spawning period there would be 2000 eggs per square meter. This number is exceeded in about 20% of the samples of *E. ringens*, 3% of the samples of *E. mordax*, 15% of the *S. sagax*, and less than 1% of the samples of *S. caerulea*.

SUMMARY

1) The numbers of eggs of *Engraulis ringens* off Peru per square meter exceed those of *Engraulis mordax* off California.

2) The numbers of eggs of *Sardinops sagax* off Peru per square meter exceed those of *Sardinops caerulea* off California.

3) Both off Peru and California the numbers of eggs from the genus *Engraulis* exceed those of the genus *Sardinops*.

4) A wide variety of demographic, behavioural and environmental factors has been discussed singly and jointly and there needs to be special research conducted to identify the most important influences. It seems plausible that the differences in numbers of eggs per square meter between the genera *Engraulis* and *Sardinops* are caused primarily by demographic differences in the populations and that the differences between the Peruvian stocks and Californian stocks are caused primarily by environmental factors in concert with behaviour.

5) Regardless of the causes of the difference in egg distribution among the four stocks off Peru and California, caution is warranted in establishing the optimum number of samples for calculating the egg mortality using the Southwest Fisheries Center Egg Production Method. It appears that more samples will be needed for a fixed precision in the Peruvian anchoveta compared with the other three stocks.

6) Some of the features distinguishing the four stocks studied here may effect the efficacy of the mortality regression method and its precision. Particularly those features implying selective predation and cannibalism (Santander et al., MS) could strongly affect the assumption of equal variance in real or porportional terms for the regression of egg abundance on time. Also environmental changes in the rate of dispersal of the eggs could also complicate regression methods which require stability of variance among the elements of the regression.

7) The degree of difference among the eggs per unit surface area, when all have likely had an origin in a compact volume for external fertilization, is likely to portend great differences in the biology of the embryonic stages and the ultimate contribution of fluctuations of position and survival during this stage to population control mechanisms.

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DETALLES TECNICOS DE UN PLAN DE CRUCERO PARA ESTIMAR LA BIOMASA DESOVANTE DE ANCHOVETA

Paul E. Smith[1], Haydeé Santander[2] y Juergen Alheit[3]

1. NOAA, National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, California 92038, U.S.A.
2. Instituto del Mar del Perú, Apartado 22, Callao, Perú
3. Programa Cooperativo Peruano-Alemán de Investigación Pesquera (PROCOPA), Instituto del Mar del Perú, Apartado 22, Callao, Perú

RESUMEN

Se presenta la metodología para diseñar un plan de crucero para estimar la biomasa desovante de anchoveta y se incluyen programas de computación en BASIC. Los programas permiten la selección de estaciones de cualquier área.

La posición de estaciones está impresa para el uso del capitán y oficiales del barco en el orden establecido por el Jefe Científico.

INTRODUCCION

En el planeamiento de un crucero es necesario cumplir varias etapas. La información biológica disponible debe acumularse y analizarse para luego determinar el número de muestras, el diseño de la red de estaciones y el plan del crucero. Por último, se debe encontrar un balance entre la cobertura máxima del área bajo investigación y el tiempo de barco disponible.

Este trabajo describe los detalles técnicos para establecer una red de estaciones, la forma de transformar los números de estación de muestreo a coordenadas geográficas y cómo dibujar un mapa del área de muestreo juntamente con la línea costera y la posición de estaciones. Todas las instrucciones están compiladas en programas de computación BASIC, para reducir el tiempo para cruceros futuros.

El crucero descrito aquí fue parte de un programa para estimar la biomasa desovante de la anchoveta peruana Engraulis ringens de acuerdo al "Método de Producción de Huevos" recientemente desarrollado en el Southwest Fisheries Center, California (Parker, 1980; Stauffer and Picquelle, 1980). Este método incluye el estimado conjunto de la producción de huevos por unidad de área del mar por unidad de tiempo y la producción de huevos por unidad de pez adulto por unidad de tiempo, para obtener un estimado instantáneo de la biomasa adulta. Este informe se refiere solamente al planeamiento de un crucero para el muestreo de los productos de desove. Basado en resultados de los cruceros y operaciones EUREKA de IMARPE entre 1965 y 1979, se determinó que alrededor de 1000 muestras de huevos debían ser colectadas en el área entre Pisco y Punta Aguja para obtener un estimado de producción de huevos con una precisión razonable (Santander, Smith y Alheit, 1982) Los detalles técnicos del planeamiento de crucero se describen en las secciones siguientes.

METODOS

El planeamiento de crucero es derivado de la carta número 22008, 33ava Edición, de la Agencia United States Defense Mapping, de fecha 8 de marzo 1980. Todas las posiciones son recomendaciones para ser ocupadas según la discreción del capitán y oficiales del barco, en lo que respecta a seguridad. El jefe científico del crucero tiene la facultad de alterar la posición de las estaciones, el orden de ocupación de las mismas, variar su número total y aumentar las que se requieran, de acuerdo a los objetivos del crucero.

La línea base del patrón de crucero, que es perpendicular a la costa, es la línea número 180, del Callao, con rumbo de 240° a través de la estación 1800.0800 en la posición 12°30.0' latitud sur y 78° 00.0' longitud oeste (Fig. 1). Se establecieron líneas paralelas a la línea 180, próximas a la frontera norte del Perú (línea 40) hasta el área de Pisco (línea 213). Estas líneas se denominarán líneas de estaciones. Cada dígito de un número de línea de estación representa 3 millas náuticas. El mismo sistema de numeración puede ser mantenido hasta el límite sur del Perú si fuera necesario. Se establecieron líneas mayores de estaciones cada 30 millas (correspondiente a 10 unidades) desde la línea de estaciones 40 a la línea de estaciones 210, para abarcar toda la zona costera del rango de desove de la subpoblación norte-central de la anchoveta peruana en años recientes. Hacia fuera de la costa líneas de estaciones de hasta generalmente 90 millas cubrieron el rango de la anchoveta mar afuera.

Las estaciones estuvieron distribuídas cada 3 millas sobre los transectos, de tal forma que cada estación es equivalente a 3 millas náuticas. La línea de estaciones "0" está ubicada en tierra, de tal forma que cada estación real tiene un número positivo. La red de estaciones de muestreo está orientada de tal forma que esta línea es paralela a la costa entre Pta. Aguja y Pisco. En cada línea de estaciones se fijó la estación próxima a la costa a una distancia no menor a 5 millas náuticas de la costa. Puesto que cada número de estación representa 3 millas, las estaciones costeras variarán de 5 a 8 millas de la costa. En el programa denominado "Planeador de Crucero" (Apéndice 1) se introducen los números de las líneas de estaciones (Instrucción 710) y para cada uno de ellos también se introduce las estaciones hacia la costa y hacia el mar (Instrucciones 730, 741) y el rumbo que sigue el barco (hacia la costa 60°, o hacia fuera de la costa 240°). En esta forma se establece una estación cada 3 millas a lo largo de cada línea de estaciones.

Se da un énfasis adicional al muestreo cerca a la costa, en relación a la distribución actual de la población de anchoveta, por líneas de estaciones más cortas que se inician también de 5 a 8 millas de la costa hasta 30 millas náuticas de la costa. En la Fig. 2 se presenta el mapa de las estaciones. Para reducir tiempo de recorrido del barco, las líneas de estaciones mayores son ocupadas consecutivamente hacia afuera y hacia adentro de la costa. Entre ellas se ocupan las líneas de estaciones cortas, intermedias. En la Fig. 2 también se muestra la dirección que debe seguirse. En la Tabla 1 se da las líneas de estaciones en orden numérico, las estaciones hacia la costa y hacia afuera de la costa, la dirección de ocupación y el orden de ocupación de la línea de estaciones, para 53 líneas. El crucero se desarrolla de sur a norte.

Para propósitos de navegación estas estaciones son convertidas a posiciones (coordenadas geográficas) usando el algoritmo de Eber and

Hewitt (1979) desarrollado para la red de estaciones CalCOFI, modificada para la red de estaciones de IMARPE (Apéndice 2. "Bitácora del Capitán"). La lista ordenada de estaciones creada por el "Planeador de Crucero" (Apéndice 1) es leída por el programa de Bitácora del Capitán, y a cada estación se le asigna una posición deseada (latitud, longitud) y orden de ocupación. La ecuación se da en las instrucciones 420 a 760. El número de la estación de referencia I9 (80) se asigna en la instrucción 440, y el número de la línea de estaciones de referencia J9 (180) en la instrucción 450. La unidad de incremento de la línea de estación (0.05° ó 3 millas náuticas) está definido en la instrucción 460 (X5); el incremento de unidad del número de estación (0.05°, 3 millas náuticas) está en la instrucción 470 (Y5). La posición geográfica del punto de referencia primaria está definido en las instrucciones 480 y 490; X5 es 78° longitud oeste y Y9 es 12.5° (12°30') latitud sur.

La Tabla 2 es un ejemplo del listado de las estaciones en el orden de ocupación deseado. Debido a que toma bastante tiempo para que el barco tome una posición exacta, hay espacios en blanco para llenarlos con las posiciones reales ocupadas en orden. Las estaciones agregadas o canceladas pueden ser anotadas en el mismo formulario.

El Apéndice 3 contiene un programa para diseñar un mapa de la línea costera peruana y las posiciones de las estaciones a ocuparse. Este programa puede ser modificado para indicar aquellas estaciones donde los huevos de anchoveta son encontrados así como alguna medida de su abundancia. Estas presentaciones visuales son de gran utilidad para adjuntarlos con los datos estadísticos de los cuales se derivan los resultados.

DISCUSION

Este plan de crucero es el resultado de análisis, ideas, discusiones y decisiones arbitrarias. Lo que continúa es una descripción de la información en la que se basa el plan de crucero.

La extensión del crucero se basa en la extensión del desove de anchoveta, detectado por Operaciones Eureka en la principal estación de desove en 1980. Para la mayor parte, las líneas mayores de estaciones se extienden más allá del desove de anchoveta. Nosotros creemos que la sobre-extensión debe ser mantenida por 2 razones principales:

1) Es posible un crecimiento de la población de anchoveta en el año intervenido y la extensión de las líneas de estaciones mayores permitirían una estimación de esta mayor extensión.

2) Se requieren muchas muestras de huevos de sardina para planificar la densidad de las estaciones para estimados futuros de biomasa en años subsecuentes. Esta extensión fuera de la costa proveerá más muestras de huevos de sardina.

La intensidad del muestreo está dado por: una muestra cada tres millas en el plano de distancia de la costa (hacia adentro y hacia afuera), una muestra cada 10 millas hacia el norte y sur y hasta 30 millas. El espaciamiento de líneas es de 30 millas fuera de la costa. Se requieren aproximadamente 1000 muestras para una estimación precisa de producción de huevos basada en el sumario estadístico de muestras colectadas con red Hensen de las pasadas 2 décadas (Santander, Smith y Alheit, 1982).

TECHNICAL DETAILS OF A CRUISE PLAN FOR THE ANCHOVETA SPAWNING BIOMASS ESTIMATE

Paul E. Smith[1], Haydeé Santander[2] and Juergen Alheit[3]

1. NOAA, National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, California 92038, U.S.A.
2. Instituto del Mar del Perú, Apartado 22, Callao, Perú
3. Programa Cooperativo Peruano-Alemán de Investigación Pesquera (PROCOPA), Instituto del Mar del Perú, Apartado 22, Callao, Perú

SUMMARY

The technical details for a cruise plan to evaluate anchovy spawning biomass in BASIC are presented here. The programs allow the selection of station on any grid.

The station positions in longitude and latitude are printed for use by the ship's captain and officers in the order the chief scientist has selected.

INTRODUCTION

Several steps are involved in the planning of a cruise. The available biological information has to be gathered and analyzed. Once the desired number of samples has been determined on the basis of this analysis, a station grid and a cruise plan have to be accomplished. It has to be compromised between a maximal coverage of the area under investigation and the available ship time.

This paper describes the technical details how to establish a station grid, how to transform the sampling station numbers to geographical coordinates and how to draw a map of the sampling area together with coastline and station positions. All instructions are compiled in BASIC computer programs in order to save time for future cruises.

The cruise reported here was part of a program to estimate de spawning biomass of the Peruvian anchoveta, Engraulis ringens, according to the recently "Egg Production Method" developed in the Southwest Fisheries Center, California (Parker, 1980; Stauffer and Picquelle, 1980). This method involves the joint estimation of the egg production per unit sea area per unit time and the egg production per unit adult fish per unit time to obtain an instantaneous estimate of the adult biomass. This report refers only to the planning of a cruise for sampling the spawning products. Based on results of EUREKA cruises of IMARPE between 1965 and 1979, it was determined that about 1000 egg samples must be collected in the area between Pisco and Punta Aguja to obtain an egg production estimate with a reasonable precision (Santander, Smith and Alheit, 1982). The technical details of the cruise planning are described in the following section.

METHODS

All cruise planning is derived from chart number 22008, 33rd Edition, United States Defense Mapping Agency dated March 8, 1980. All positions are recommendations to be occupied at the discretion of the ship's captain and officers with regard to safety. The chief scientist on the cruise is traditionally given the power to alter the station positions, the order in which the stations are occupied, the total number of stations, and the addition of stations, as requiered under the objectives of the cruise.

The base line of the cruise pattern, which is perpendicular to the coast, is line number 130 through Callao on a course of 240° through station 1800.0800 at 12°30.0' south latitude and 78°00.0' west longitude (Fig. 1). Lines parallel to line 180 were established from near the northern border of Peru (line 40) to the area of Pisco (line 213). These lines will be called station lines. Each digit of a station line number represents 3 nautical miles. The same numbering system can be maintained to the southern border of Peru when required. Major station lines were established each 30 miles (correspond to 10 line units) from station line 40 to station line 210 to encompass all of the coast-wide range of spawning of the north-central subpopulation of the Peruvian anchoveta in recent years. The offshore range of the anchoveta was encompassed with stations proceeding generally 90 miles to sea.

On the station lines, the stations were spread 3 miles from each other, so that each station number is equivalent to 3 nautical miles. The line of the "0" stations is inland so that each station number is positive. The sampling grid is orientated so that this line is parallel to the coast between Punta Aguja and Pisco. On each station line was established a nearshore station with a whole number not closer than 5 nautical miles from the nearest land. Thus since each number represents 3 miles, the nearshore stations will vary from 5 to 8 miles offshore. In the program called "Cruise Planner" (Appendix 1) the station line numbers are entered (Instruction 710) and for each station line number the shoreward and seaward stations are entered (Instruction 730, 741) and the direction that the ship is to proceed (onshore 60°, or offshore 240°). In this way a station is established each 3 miles along each station line.

Additional emphasis to nearshore sampling which conforms to the present population distribution of the anchoveta is provided by shorter station lines starting as well 5 to 8 miles offshore out to 30 nautical miles further offshore. Figure 2 is the map of the stations. To save ship running time the long station lines are occupied consecutively, away from shore and towards the shore. Between them, short intermediate station lines are occupied. The way the ship has to proceed is demonstrated also in Fig. 2. The list of the station lines in numeric order, the onshore and offshore stations, the direction of occupancy and the station line order of occupancy is given for 53 lines in Table 1 for the recommended cruise plan. The cruise proceeds from south to north.

For navigational purposes these stations are converted to positions (geographical coordinates) using the algorithm of Eber and Hewitt (1979) developed for the CalCOFI grid as modified for IMARPE grid (Appendix 2, "Captain's Log"). The ordered list of stations created by "Cruise Planner" (Appendix 1) is read by the Captain's Log program, and each station is assigned a desired position (latitude, longitude) and order of occupancy. The equation is located in instruction 420 through 760. The reference station number, I9 (80), is assigned in instruction 450. The unit station line number increment

(0.05° or 3 nautical miles) is defined in instruction 460 (X5); the unit station number increment (0.05°, 3 nautical miles) is in instruction 470 (Y5). The geographic position of the primary reference point is defined in instructions 480 and 490; X5 is 78° west longitude and Y9 is 12.5° (12°30') south latitude. Table 2 is an example of a listing of the stations in the desired order of occupancy. Because it is too time consuming to position a ship at an exact position there are blanks for filling out the actual position occupied in the actual order. Stations added or cancelled can be noted on the same sheet.

Appendix 3 contains a program to draw a map of the Peruvian coastline and the positions of the stations to be occupied. This program may be modified to indicate those stations where anchovy eggs are found and some measure of their abundance. These visual presentations are valuable adjunct to the statistical data from which the results are derived.

DISCUSSION

This cruise plan is the result of analysis, judgement, discussion and arbitrary decisions. What follows is a description of the information on which the cruise plan was based.

The extent of the cruise is based on the extent of the anchovy spawning as detected by Eureka cruises in the principal spawning season in 1980. For the most part, the long station lines extend beyond the anchoveta spawning. We believe the overextention should be maintained for two main reasons: 1) growth of the anchovy population is possible in the intervening year and the extention of the major station lines would allow an estimation of the expanding coverage; 2) many samples of sardine eggs are needed to plan the station density for future sardine biomass estimates in subsequent years. These offshore extentions will provide more samples of sardine eggs.

The intensity of sampling is one sample each three miles in the offshore/onshore plane, each 10 miles north and south at the coast and out for 30 miles. Line spacing is 30 miles offshore. Approximately 1000 samples are required for precise estimation of egg production based on statistical summary of Hensen net samples of the past two decades (Santander, Smith and Alheit, 1982).

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Figura 1. Patrón del crucero: línea base y de estaciones.
Figure 1. Cruise pattern: base and stations line.

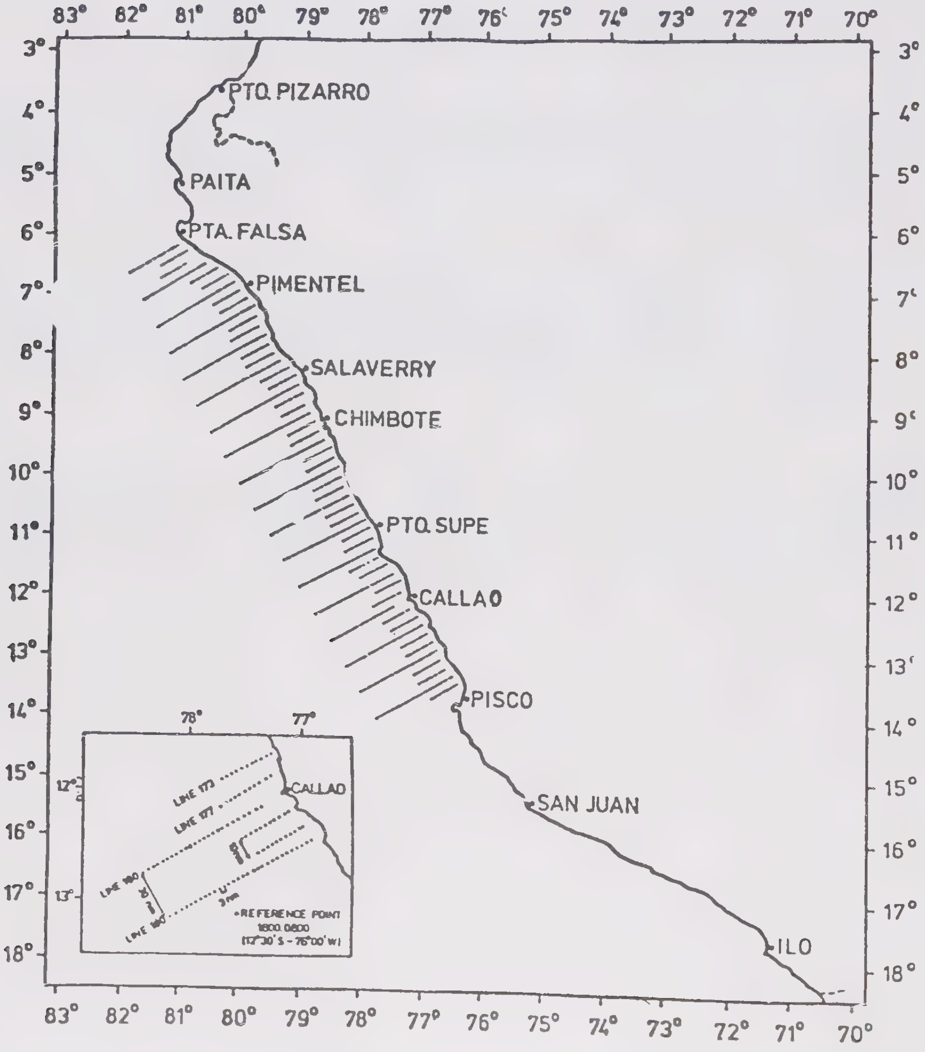

Figura 2. Carta de estaciones y trayecto de ocupación.
Figure 2. Station chart and track for occupation.

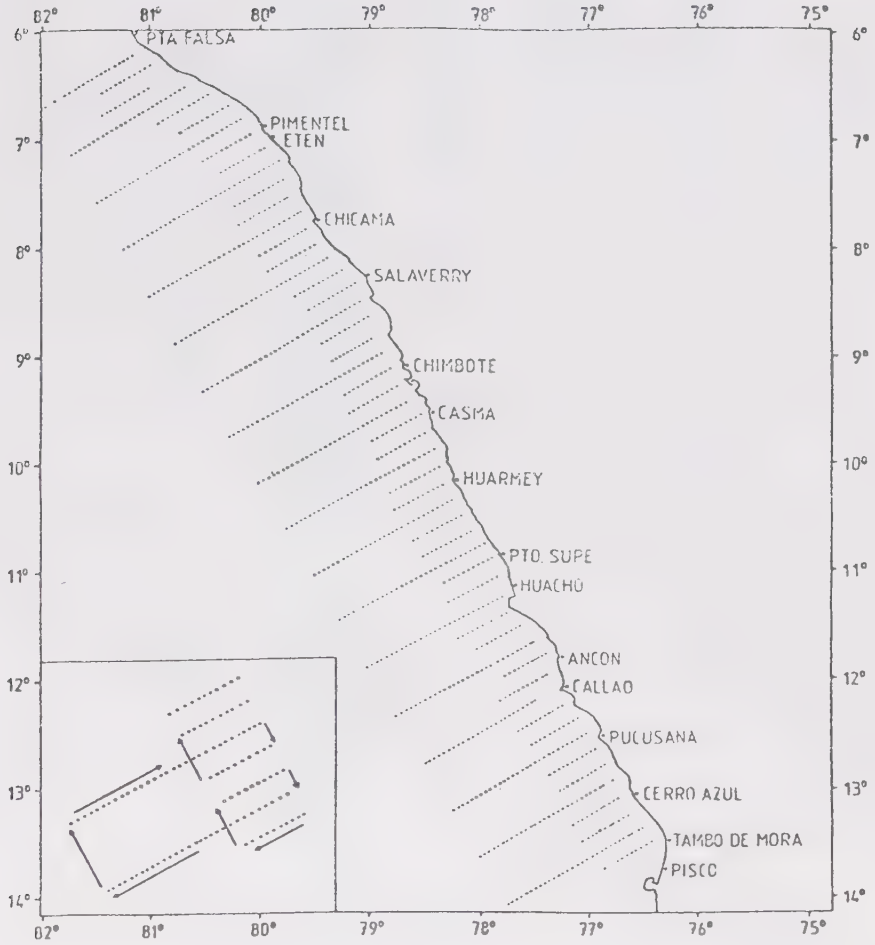

Tabla 1. Crucero 8108 - Sumario de líneas de estaciones.
Table 1. Cruise 8108 - Station line summary.

Número de líneas Line number	Estación cercana Inshore station	Estación lejana Offshore station	Dirección Direction	Orden de línea Line order
40	71	90	Onshore	52
43	69	79	Offshore	53
47	71	81	Onshore	50
50	65	90	Offshore	51
53	62	72	Offshore	49
57	60	70	Onshore	48
60	59	90	Onshore	46
63	59	69	Offshore	47
67	58	68	Onshore	44
70	57	90	Offshore	45
73	58	68	Offshore	43
77	59	69	Onshore	42
80	58	90	Onshore	40
83	59	69	Offshore	41
87	59	69	Onshore	38
90	58	90	Offshore	39
93	57	67	Offshore	37
97	56	66	Onshore	36
100	57	90	Onshore	34
103	57	67	Offshore	35
107	57	67	Onshore	32
110	58	90	Offshore	33
113	58	68	Offshore	31
117	59	69	Onshore	30
120	59	90	Onshore	28
123	58	68	Offshore	29
127	59	69	Onshore	26
130	59	90	Offshore	27
133	60	70	Offshore	25
137	61	71	Onshore	24
140	61	90	Onshore	22
143	61	71	Offshore	23
147	61	71	Onshore	20
150	60	90	Offshore	21
153	60	70	Offshore	19
157	61	71	Onshore	18
160	62	90	Onshore	16
163	63	73	Offshore	17
167	61	71	Onshore	14
170	61	90	Offshore	15
173	60	70	Offshore	13
177	62	72	Onshore	12
180	66	90	Onshore	10
183	62	72	Offshore	11
187	61	71	Onshore	8
190	61	90	Offshore	9
193	61	71	Offshore	7
197	61	71	Onshore	6
200	61	90	Onshore	4
203	62	72	Offshore	5
207	62	72	Onshore	2
210	61	90	Offshore	3
213	61	71	Offshore	1

Tabla 2. Lista de ubicación de estaciones ocupadas y proyectadas.
Table 2. List of station positions, occupied and projected.

CAPITAN	JEFE DE NAVEGACION	MES(ES) AÑO	BUQUE	R.	TOTAL	CRUCERO
		81 AUG-SEP	HUMBOLDT	1	62	8108 AH

ESTACION	ORDEN OCUP. ESTAC.	POSICION PROYECTADA		POSICION REAL		FECHA Y HORAS				OBSERVACIONES SCHEDULED STATION ORDER
		LAT. S	LONG. W	LAT. S	LONG. W	DIA Y MES	LLEGADA	PARTIDA		
213 61		13 28.0	76 18.5							1
213 62		13 29.5	76 21.2							2
213 63		13 31.0	76 23.8							3
213 64		13 32.5	76 26.5							4
213 65		13 34.0	76 29.2							5
213 66		13 35.5	76 31.8							6
213 67		13 37.0	76 34.5							7
213 68		13 38.5	76 37.1							8
213 69		13 40.0	76 39.8							9
213 70		13 41.5	76 42.4							10
213 71		13 43.0	76 45.1							11
207 72		13 27.4	76 57.9							12
207 71		13 25.9	76 55.2							13
207 70		13 24.4	76 52.6							14
207 69		13 22.9	76 49.9							15

'APPENDIX #1 CRUISE PLANNER

```
          100 INIT
          110 J=0
          120 PRINT "                    CRUISE PLANNER"
          130 PRINT "JJJJ"
          140 REM CFEATE CRUISE FILE
          150 GOSUB 420
          160 REM OPEN PICK LIST FILE
          170 OPEN F$;5,'U',Z$
          180 PRINT 'ENTER 1- INPUT LINE, STATION,TYPE'
          190 PRINT '       2- PICK STATION FROM LIST'
          200 PRINT '       3- PICK STATIONS FROM LIST AND CHANGE STATION'
          210 PRINT '       4- CHANGE FILE TO PICK STATION FROM'
          220 PRINT '       5- END'
          230 INPUT W
          240 GOSUB W OF 710,260,920,660,400
          250 GOTO 160
          260 PRINT "ENTER THE NUMBER OF THE STATION (OR 0 FOR A SERIES OF STATI
ONS"
          270 INPUT S9
          280 IF S9=999 THEN 400
          290 IF S9=0 THEN 330
          300 READ #1,S9:L,S,T
          310 GOSUB 620
          320 RETURN
          330 PRINT 'ENTER THE.# OF THE FIRST STATION, # OF LAST STATION, STEP'
          340 INPUT S7,S8,S5
          350 FOR I=S7 TO S8 STEP S5
          360 READ #1,I:L,S,T
          370 GOSUB 620
          380 NEXT I
          390 RETURN
          400 CLOSE
          410 END
          420 PRINT "ENTER CRUISE (8012JD)"
          430 INPUT C$
          440 F$="@STATIONS/"
          450 D$=SEG(C$,5,2)
          460 F$=F$&D$
          480 F$=F$&D$
          490 PRINT F$
          500 PRINT "ENTER THE NUMBER OF STATIONS TO BE OCCUPIED"
          510 INPUT R9
          520 CALL 'FILE',0,F$,R$
          530 IF LEN(R$)=0 THEN 600
          540 PRINT "FILE ALREADY EXISTS - - DO YOU WANT TO DESTROY IT Y/N"
          550 INPUT Y$
          560 IF Y$='Y' THEN 590
          570 PRINT "PROGRAM TERMINATED"
          580 END
          590 KILL F$
          600 CREATE F$,'U';R9+1,50
          610 RETURN
          620 REM ADD STATIONS TO NEW CRUISE LIST
          630 J=J+1
          640 WRITE #5,J:L,S,T
          650 RETURN
          660 PRINT "ENTER FILE TO PICK STATIONS FROM"
          670 INPUT J$
          680 CLOSE 1
          690 OPEN J$;1,'R',Z$
          700 RETURN
          710 PRINT "LINE NUMBER?"
          720 INPUT L
          730 PRINT "SHOREWARD STATION?"
          740 INPUT S1
          741 PRINT "SEAWARD STATION?"
          742 INPUT S2
          750 PRINT "PROCEEDING ONSHORE (2) OR OFFSHORE (1)?"
          760 INPUT S9
          770 IF S9=2 THEN 790
          780 GOTO 850
          790 FOR I=S2 TO S1 STEP -1
          800 S=I
          810 T=1
          820 GOSUB 620
          830 NEXT I
          840 GOTO 710
          850 FOR I= S1 TO S2
          860 S=I
          870 T=1
          880 GOSUB 620
          890 NEXT I
          900 GOTO 710
          910 RETURN
          920 PRINT "ENTER THE NUMBER OF THE STATION (OR 0 FOR A SERIES OF STATI
ONS"
          930 INPUT S9
          940 IF S9 = 0 THEN 980
          950 READ #1,S9:L,S,T
          960 GOSUB620
          970 RETURN
          980 PRINT "ENTER THE # OF THE FIRST STATION # OF LAST STATION AND STEP
```

```
990 INPUT S7,S8,S5
1000 PRINT "ENTER NEW STATION NUMBER"
1010 INPUT N9
1020 FOR I=S7 TO S8 STEP S5
1030 READ #1,I:L,S,T
1040 S=N9
1050 GOSUB 620
1060 NEXT I
1070 RETURN
1080 OPEN '@STATIONS/JD8104',4,'U',Z$
1090 FOR O9 = 1 TO 50
1100 READ #4,O9:L,S,T
1110 PRINT O9,L,S,T
1120 NEXT O9
1130 CLOSE
```

'APPENDIX 2 CAPTAIN'S LOG

```
1 GOTO 100
4 GOTO 540
100 INIT
110 REM PERUVIAN CAPTAIN'S LOG PROGRAMMED BY RICH CHARTER
120 REM MODIFIED FOR PERUVIAN COAST AND SURVEY OBJECTIVES
130 REM BY PAUL SMITH
140 R9=0
150 SET DEGREES
160 PRINT @32,26:2
170 I4=0
180 W=0
190 PRINT "ENTER MONTH (OCT-OCT)"
200 INPUT M$
210 PRINT "INPUT YEAR (80)"
220 INPUT Y$
230 PRINT "INPUT VESSEL"
240 INPUT V$
250 PRINT "ENTER CRUISE (8018 JD)"
260 INPUT D$
270 E$=SEG(D$,1,4)
280 F$=SEG(D$,6,2)
290 G$=F$&E$
300 I$="@STATIONS/"&G$
310 PRINT "ENTER CAPTAIN'S NAME"
320 INPUT N$
330 PRINT "ENTER FIRST MATE'S NAME"
340 INPUT O$
350 PRINT "ENTER SECOND MATE'S NAME"
360 INPUT H$
370 PRINT "DO YOU WANT TO READ STATIONS FROM DISK FILE Y/N"
380 INPUT W$
390 IF W$="N" THEN 420
400 W=1
410 GOSUB1710
420 REM PROCOPA STN NO. TO LAT-LON
430 B$='POSITION
440 I9=80
450 J9=180
460 X5=0.05
470 Y5=-0.05
480 X9=78
490 Y9=-12.5
500 DELETE P3,P4,P5,P6,P7,P8

510 DIM P3(15),P4(15),P5(15),P6(15),P7(15),P8(15),R8(15)
520 REM FNZ IS THE MERCATOR TRANSFORM
530 DEF FNZ(T1)=LOG(TAN(45+T1/2))*180/PI-0.387815*SIN(T1)
540 I4=0
550 OPEN I$,1,'R',A$
560 FOR Q = 1 TO 15
570 IF W THEN 620
580 PRINT 'ENTER LINE NO., STN NO., STATION TYPE ';
590 INPUT L,S,T
600 REM PRINT @33:L,S,T
610 GOTO 650
620 ON EOF (1) THEN 860
630 R9=R9+1
640 READ #1,R9:L,S,T
650 INF L=0 THEN 860
660 Y7=Y5*(L-J9)
670 X7=X5*(S-I9)
680 R1=Y9+Y7*COS(30)
690 R2=X9+(FNZ(R1)-FNZ(Y9))*TAN(30)
700 Y=R1-X7*SIN(30)
710 X=R2+(FNZ(R1)-FNZ(Y))/TAN(30)
720 L1=INT(ABS(Y))
730 M1=(ABS(Y)-L1)*60
740 L2=INT(X)
750 M2=(X-L2)*60
```

```
760 PRINT USING 770:B$,L1,M1,'S',L2,M2,'W',L,'.',B
770 IMAGE 10A,3D,1X,2D.D,1A,2X,3D,1X,2D.D,1A,5X,3D,1A,3D
780 P3(Q)=L
790 P4(Q)=B
800 P5(Q)=L1
810 P6(Q)=M1
820 P7(Q)=L2
830 P8(Q)=M2
840 R8(Q)=R9
850 GOTO930
860 P3(Q)=0
870 P4(Q)=0
880 P5(Q)=0
890 P6(Q)=0
900 P7(Q)=0
910 P8(Q)=0
920 R8(Q)=0
930 NEXT Q
940 GOTO 1090
950 END
960 REM INVERSE MERCATOR TRANSFORM
970 REM THIS IS AN INTERATIVE PROCEDURE IN WHICH FNZ(T1) IS TAKEN AS
980 REM THE FIRST APPROXIMATION TO T1.  IT CONVERGES TO WITHIN .0001
990 REM DEG (.006 MIN) OF T1 AFTER ONE ITERATION. A GREATER ACCURACY
!000 REM CAN BE OBTAINED BY APPROPRIATE MODIFICATION OF THE PROCEDURE
.010 REM TO PERFORM MORE ITERATIONS.
.020 T2=F1*PI/180
1030 T1=F1
1040 FOR B=1 TO 3
1050 T1=2*(ATN(EXP(T2+0.0067686*SIN(T1)))-45)
1060 NEXT B
1070 R1=T1
1080 RETURN
1090 PRINT "PUT NEW PAGE ON AND HIT THE RETURN KEY"
1100 I4=I4+1
1110 INPUT Z$
1120 PRINT@8,17:1.3,2
1130 MOVE@8:0.1,66.8
1140 PRINT@8:N$
1150 MOVE@8:20,68.15
1160 PRINT@8:O$
1170 MOVE@8:20,66.25
1180 PRINT@8:H$
1190 MOVE@8:44,68.3
1200 PRINT@8,7:
1210 S=2
1220 PRINT@8:M$
1230 MOVE@8:40,68.3
1240 S=1.6
1250 PRINT@8,17:1.56,2.5
1260 PRINT@8:Y$
1270 PRINT@8,7:
1280 MOVE@8:58.85,68.3
1290 S=2
1300 PRINT@8,17:1,2
1310 PRINT@8:V$
1320 PRINT@8,17:0.95,2
1330 MOVE@8:78,68.3
1340 PRINT@8:USING '2D':I4
1350 MOVE@8:83,68.3
1360 PRINT@8: USING '2D':I6
1370 MOVE@8:89.45,68.3
1380 S=2
1390 PRINT@8,17:1.25,2
1400 PRINT@8:D$
1410 MOVE@8:78.5,62
1420 PRINT@8,17:0.75,1.5
1430 PRINT@8:'SCHEDULEDJHHHHHHHHHSTATION ORDER'
1440 Q9=60.45
1450 PRINT@8,17:0.95,2
1460 FOR Q8=1 TO 15
1470 Q9=Q9-3.45
1480 MOVE@8:-5.5,Q9
1490 IF P3(Q8)=0 THEN 1620
1500 S=1.5
1510 PRINT@8: USING '3D,3X,3D':P3(Q8),P4(Q8)
1520 MOVE@8:18,Q9
1530 S=1.3
1540 PRINT@8,17:0.95,2
1550 PRINT@8:USING '2D,1X,2D.D':P5(Q8),P6(Q8)
1560 MOVE@8:26.25,Q9
1570 S=1.3
1580 PRINT@8: USING '3D,1X,2D.D':P7(Q8),P8(Q8)
1590 MOVE@8:79,Q9
1600 PRINT@8: USING '3D':R8(Q8)
1610 GOTO1630
1620 IF I4=I6 THEN 1650
1630 NEXT Q8
1640 GOTO 560
1650 PRINT@32,26:0
1660 PRINT "THE END"
1670 END
1680 GIN@8,Z5,Z6
1690 PRINT Z5,Z6
```

```
1700 GOTO 1680
1710 REM FIND THE NUMBER OF STATIONS AND PAGES REQUIRED
1720 OPEN I$;1,'R',A$
1730 I5=1
1740 E9=TYP(1)
1750 IF E9=1 OR E9=0 THEN 1800
1760 ON EOF (1) THEN 1800
1770 READ #1,I5:L,S,T
1780 I5=I5+1
1790 GOTO 1740
1800 I5=I5-1
1810 CLOSE
1820 I6=I5/15
1830 I6=INT(I6)
1840 IF I6*15=I5 THEN 1860
1850 I6=I6+1
1860 RETURN
```

'APPENDIX 3 PERUVIAN COASTLINE PLOT

```
100 REM PROGRAM TO PLOT PERUVIAN COASTLINE WITH STATIONS
110 PRINT "DO YOU WANT MAP ON SCREEN '1' OR PLOTTER '2'";
111 INPUT Q
112 IF Q<2 THEN 115
113 Q1=0
114 GOTO 120
115 Q1=32
120 PAGE
130 VIEWPORT 10,85,10,100
140 DIM W5(120)
150 WINDOW -80,-70,-18,-3
160 AXIS@Q1:-1,1
170 AXIS@Q1:-1,1,-70,-3
180 FIND 2
190 READ@33:T$
200 READ@33:B2,B,W1,W2,W3,W4
210 READ@33:W5(1),W5(2)
215 MOVE@Q1:-79.8,-3
220 DRAW@Q1:-W5(2),W5(1)
230 FOR I= 3 TO 2*B STEP 2
235 ON EOF (0) THEN 250
240 READ@33:X,Y
250 DRAW@Q1:-Y,X
260 NEXT I
610 MOVE@Q1:-90,-5.2
620 PRINT@Q1:' 5'
630 MOVE@Q1:-90,10.2
640 PRINQ1:'10'
650 MOVE@Q1:-90,-15.2
660 PRINT@Q1:'15'
690 MOVE@Q1:-85.5,-19
700 PRINT@Q1:'85'
710 MOVE@Q1:-80.5,-19
720 PRINT@Q1:'80'
730 MOVE@Q1:-75.5,-19
740 PRINT@Q1:'75'
750 MOVE@Q1:-80,-5
760 RDRAW@Q1:0.5,0
770 MOVE@Q1:-70,-5
780 RDRAW@Q1:-0.5,0
790 MOVE@Q1:-80,-10
800 RDRAW@Q1:0.5,0
810 MOVE@Q1:-70,-10

820 RDRAW@Q1:-0.5,0
830 MOVE@Q1:-80,-15
840 RDRAW@Q1:0.5,0
850 MOVE@Q1:-70,-15
860 RDRAW@Q1:-0.5,0
870 MOVE@Q1:-85,-18
880 RDRAW@Q1:0,0.3
890 MOVE@Q1:-85,-3
900 RDRAW@Q1:0,-0.3
910 MOVE@Q1:-80,-18
920 RDRAW@Q1:0,0.3
930 MOVE@Q1:-80,-3
940 RDRAW@Q1:0,-0.3
950 MOVE@Q1:-75,-18
960 RDRAW@Q1:0,0.3
970 MOVE@Q1:-75,-3
980 RDRAW@Q1:0,-0.3
```

```
1200 MOVE@Q1:-80.9,-5.4
1210 PRINT@Q1:'PAITA'
1220 MOVE@Q1:-78.36,-9
1230 PRINT@Q1:'CHIMBOTE'
1240 MOVE@Q1:-77,-12
1250 PRINT@Q1:'CALLAO'
1260 MOVE@Q1:-76.13,-13.42
1270 PRINT@Q1:'PISCO'
1280 MOVE@Q1:-71.2,-17.30
1290 PRINT@Q1:'ILO'
1300 GOTO 1330
1310 GOTO 1730
1320 INIT
1330 R9=0
1340 SET DEGREES
1350 PRINT@32,26:2
1360 I4=0
1370 W=0
1450 D$="8109 AH"
1460 E$=SEG(D$,1,4)
1470 F$=SEG(D$,6,2)
1480 G$=F$&E$
1490 I$="@STATIONS/"&G$
1570 W$="Y"
1580 IF W$="N" THEN 1610
1590 W=1
1600 GOSUB 2890
1610 REM PROCOPA STN NO. TO LAT-LON
1620 B$='POSITION'
1630 I9=80
1640 J9=180
1650 X5=0.05
1660 Y5=-0.05
1670 X9=78
1680 Y9=-12.5
1690 DELETE P3,P4,P5,P6.P7,P8
1700 DIM P3(15),P4(15),P5(15),P6(15),P7(15),P8(15),R8(15)
1710 REM FNZ IS THE MERCATOR TRANSFORM
1720 DEF FNZ(T1)=LOG(TAN(45+T1/2))*180/PI-0.387815*SIN(TI)
1730 I4=0
1740 OPEN I$;1,'R',A$
1750 FOR Q=1 TO 15
1760 IF W THEN 1810
1770 PRINT 'JENTER LINE NO., STN NO., STATION TYPE ';
1780 INPUT L,S,T
1790 REM PRINT @33:L,S,T
1800 GOTO 1840
1810 ON EOF(1) THEN 2050
1820 R9=R9+1
1830 READ #1,R9:L,S,T
1840 IF L=0 THEN 2050
1850 Y7=Y5*(L-J9)
1860 X7=X5*(S-I9)
1870 R1=Y9+Y7*COS(30)
1880 R2=X9+(FNZ(R1)-FNZ(Y9))*TAN(30)
1890 Y=R1-X7*SIN(30)
1900 X=R2+(FNZ(R1)-FINZ(Y))/TAN(30)
1910 MOVE@Q1:-X,Y
1920 DRAW@Q1:-X,Y
1930 L1=INT(Y)
1940 M1=(Y-L1)*60
1950 L2=INT(X)
1960 M2=(X-L2)*60
1970 P3(Q)=L
1980 P4(Q)=S
1990 P5(Q)=L1
2000 P6(Q)=M1
2010 P7(Q)=L2
2020 P8(Q)=M2
2030 R8(Q)=R9
2040 GOTO 2120
2050 P3(Q)=0
2060 P4(Q)=0
2070 P5(Q)=0
2080 P6(Q)=0
2090 P7(Q)=0
2100 P8(Q)=0
2110 R8(Q)=0
2120 NEXT Q
2130 GOTO 2280
2140 END
2150 REM INVERSE MERCATOR TRANSFORM
2160 REM THIS IS AN ITERATIVE PROCEDURE IN WHICH FNZ(T1) IS TAKEN AS
2170 REM THE FIRST APPROXIMATION TO T1. IT CONVERGES TO WITHIN .0001
2180 REM DEG (.006 MIN) OF T1 AFTER ONE ITERATION.  GREATER ACCURACY
2190 REM CAN BE OBTAINED BY APPROPRIATE MODIFICATION OF THE PROCEDURE
2200 REM TO PERFORM MORE ITERATIONS.
2210 T2=F1*PI/180
```

```
2220 T1=F1
2230 FOR B= 1 TO 3
2240 T1=2*(ATN(EXP(T2+0.0067686*SIN(T1)))-45)
2250 NEXT B
2260 R1=T1
2270 RETURN
2280 I4=I4+1
2290 GOTO 1750
2300 PRINT@8,17:1.3,2
2310 MOVE@8:0.1,66.8
2320 PRINT@8:N$
2330 MOVE@8:20,68.15
2340 PRINT@8:O$
2350 MOVE@8:20,66.25
2360 PRINT@8:H$
2370 MOVE@8:44,68.3
2380 PRINT@8,7:
2390 S=2
2400 PRINT@8:M$
2410 MOVE@8:40,68.3
2420 S=1.6
2430 PRINT@8,17:1.56,2.5
2440 PRINT@8:Y$
2450 PRINT@8,7:
2460 MOVE@8:58.85,66.45
2470 S=2
2480 PRINT@8,17:1,2
2490 PRINT@8:V$
2500 PRINT@8,17:0.95,2
2510 MOVE@8:78,67.2
2520 PRINT@8: USING '2D'::I4
2530 MOVE@8:83,67.2
2540 PRINT@8: USING '2D':I6
2550 MOVE@8:89.45,67.4
2560 S=2
2570 PRINT@8,17:1.25,2
2580 PRINT@8:D$
2590 MOVE@8:78.5,62
2600 PRINT@8,17:0.75,1.5
2610 PRINT@8:'SCHEDULEDJHHHHHHHHHSTATIONJHHHHHHHORDER'
2620 Q9=57
2630 PRINT@8,17:0.95,2
2640 FOR Q8=1 TO 15
2650 Q9=Q9-3.4
2660 MOVE@8:-5.5,Q9
2670 IF P3(Q8)=0 THEN 2800
2680 S=1.5
2690 PRINT@8: USING '3D,3X,3D':P3(Q8),P4(Q8)
2700 MOVE@8:18,Q9
2710 S=1.3
2720 PRINT@8,17:0.95,2
2730 PRINT@8: USING '2D,1X,2D.D':P5(Q8),P6(Q8)
2740 MOVE@8:26.25,Q9
2750 S=1.3
2760 PRINT@8: USING '3D,1X,2D.D':P7(Q8),P8(Q8)
2770 MOVE@8:79,Q9
2780 PRINT@8: USING '3D': R8(Q8)
2790 GOTO 2810
2800 IF I4=I6 THEN 2830
2810 NEXT Q8
2820 GOTO 1750
2830 PRINT@32,26:0
2840 PRINT "THE END"
2850 END
2860 GIN@8:Z5,Z6
2870 PRINT Z5,Z6
2880 GOTO2860
2890 REM FIND THE NUMBER OF STATIONS AND PAGES REQUIRED
2900 OPEN I$;1,'R',A$
2910 I5=1
2920 E9=TYP(1)
2930 IF E9=1 OR E9=0 THEN 2980
2940 ON EOF (1) THEN 2960
2950 READ #1,I5:L,S,T
2960 I5=I5+1
2970 GOTO 2920
2980 I5=I5-1
2990 CLOSE
3000 I6=I5/15
3010 I6=INT(I6)
3020 IF I6*15=I5 TH3N 3040
3030 I6=I6+1
3040 RETURN
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8350

CHANGES IN SIZE OF THREE DOLPHIN (*STENELLA* SPP.) POPULATIONS IN THE EASTERN TROPICAL PACIFIC

TIM D. SMITH[1]

ABSTRACT

Dolphins from three populations, one of *Stenella attenuata* and two of *S. longirostris*, have been killed incidentally in the yellowfin tuna purse seine fishery in the eastern tropical Pacific, two populations since about 1959 and the other since about 1969. Size changes in these populations are estimated from numbers killed each year, population size estimates in 1979, and net recruitment rates. Ranges of values for some parameters are considered, accounting for some uncertainties. Assuming central values of the ranges of maximum net recruitment rate (3%) and the population level giving maximum net productivity (65%), one *S. longirostris* population, the eastern spinner dolphin, is near 20% of pre-exploitation levels; the *S. attenuata* population, the northern offshore spotted dolphin, is between 35 and 50%; and the second *S. longirostris* population, the whitebelly spinner dolphin, is between 58 and 72% of pre-exploitation levels.

Purse seine fishing for tuna in the eastern tropical Pacific often involves dolphins found in association with yellowfin tuna. Tuna fishermen pursue and capture the dolphin-yellowfin tuna complex, releasing the dolphins from the net while retaining the tuna (Green et al. 1971). Mortality of dolphins occurs incidental to this fishing process.

Purse seine fishermen were using dolphin schools to catch tuna by 1959; there is anecdotal information suggesting limited use as early as the 1940's (anonymous reviewer). Starting in the mid-1960's the Bureau of Commercial Fisheries, predecessor of the National Marine Fisheries Service (NMFS), conducted limited research to document the situation and to collect data on numbers and kinds of dolphins killed. This research expanded in the 1970's, especially after passage of the Marine Mammal Protection Act (MMPA) of the United States in 1972, and continues. Substantial research efforts were mounted to assess the status of the dolphin stocks and to develop procedures for reducing incidental mortality and injury.

Two assessments of the condition of dolphin populations involved in the yellowfin tuna purse seine fishery have been completed in recent years.[2,3] I describe the results of the latest assessment of the three populations most affected by the fishery; calculation of population sizes from 1959 through 1978 is emphasized, based on estimates of the population size in 1979, on annual numbers killed from 1959 through 1978, and on net recruitment rates. These results, based on data available through the end of 1980, do not necessarily represent NMFS policy, which involves additional considerations. A third assessment of these populations is scheduled for 1984 and will include information since 1980.

POPULATION MODEL

Methods developed in 1976 (footnote 2) for estimating pre-exploitation abundance are based on a simple recursive relationship

$$N_{t+1} = N_t - K_t + R_t\,(N_t - \tfrac{1}{2}K_t),$$

where t denotes the year; N, the abundance; K, the number of animals killed; and R, the net recruitment rate. This model assumes that the population size in the next year is simply the present population size, minus the present incidental kill, plus the net number of individuals recruited to the population during the year. This latter quantity is taken to be the net recruitment

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[1] Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, Calif.; present address: Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

[2] Southwest Fisheries Center La Jolla Laboratory. 1976. Report of the workshop on stock assessment of porpoises involved in the eastern Pacific yellowfin tuna fishery. Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-76-29, 53 p.

[3] Smith, T. D. (editor). 1979. Report of the workshop on status of porpoise stocks, La Jolla, Calif., 27-31 August 1979. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-70-41, 120 p.

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rate (birth rate less natural death rate) multiplied by the number of animals actually reproducing in a given year. The number of reproducing animals is approximated by assuming that one-half the animals killed in a year reproduce before dying. Solving this relationship for N_t, one obtains

$$N_t = \frac{N_{t+1} + \frac{1}{2}K_t}{1 + R_t} + \frac{1}{2}K_t. \qquad (1)$$

Repeatedly applying this equation to estimate the population size for any number of years (s) prior to the year (c) for which an independent estimate of population size (N_c) is available yields in general

$$N_s = \frac{N_c}{\prod_{i=1}^{s}\left(1 + R_i\right)} + \sum_{j=1}^{s} \frac{K_j\left(1 + \frac{1}{2}R_j\right)}{\prod_{i=j}^{s}\left(1 + R_i\right)}. \qquad (2)$$

The 1979 workshop (footnote 3) extended this procedure by calculating the recruitment rate R_i, i years prior to the present, using the density-dependent relationship (Allen 1981)

$$R_i = R_m\left\{1 - \left(\frac{N_i}{N_p}\right)^{z}\right\}. \qquad (3)$$

N_p is the estimated population size at the beginning of the first year of exploitation, p years earlier; R_m, the maximum net recruitment rate; Z, the density-dependent exponent; and N_i and N_p, estimated from Equation (2). Because N_p in Equation (3) is not known until the series in Equation (2) has been calculated, an iterative procedure is required to solve the equations for historical population size. Equations (1) and (3) together form a special case of the generalized production model of Pella and Tomlinson (1969).

In Equation (3) the net recruitment rate is maximum (R_m) when the population size approaches zero, decreasing to zero as the population size approaches N_p. Z determines the population size at which the rate of change of the population is maximum, the maximum net productivity level (*MNPL*). The values of Z correspond to the *MNPL* approximately as (Polacheck 1982)

$$MNPL = \frac{N_p}{\left(1 + Z\right)^{1/Z}}. \qquad (4)$$

If $Z = 1$, then the *MNPL* is one-half the equilibrium population size; if Z is >1, then *MNPL* is greater than one-half the equilibrium size. The fraction of the maximum reproductive rate, R_m, realized at a given population size, increases as the value of Z increases.

Statistical properties of the estimate of N_p and the ratio N_c/N_p are examined in detail in Smith and Polacheck (1979), wherein methods are developed for calculating the variances. Tests of sensitivity of the estimates of N_p to the values N_c, K_t, and R_m show that the estimates are most sensitive to the value of present abundance and least sensitive to the net recruitment rate. Examination via simulation of the shape of the sampling distribution shows that if N has a symmetrical sampling distribution, then so does the estimate N_p.

Several estimates of each parameter required by the model are available in working documents and technical memoranda prepared by the staff of the Southwest Fisheries Center. I rely on the most current estimates, primarily minor revisions of those used by the 1979 workshop, with reference to papers describing earlier estimates as needed to document methods.

POPULATIONS

Populations affected most by the yellowfin tuna purse seine fishery are of the genus *Stenella*, and are found in the area from just south of the Equator to an approximate lat. 20°N and west from the Mexican and Central American coasts to an approximate long. 150°W. Two populations of spotted dolphins, *S. attenuata*, and three populations of spinner dolphins, *S. longirostris*, are found in this region.

The two spotted dolphin populations are referred to as "offshore" and "coastal" forms. The coastal spotted dolphin population occurs nearshore and around islands, while the offshore spotted dolphin ranges from nearshore to an approximate long. 150°W. The two forms overlap in range near the coast.

Perrin (1975) distinguished these two forms of *S. attenuata* morphologically. He noted that 1) the larger coastal form occurs seaward to 50 km while the offshore form occurs as nearshore as 20 km, and 2) the coastal form was involved in only 7 of 1,373 purse seine sets on dolphins observed between 1971 and 1974. Additional data collected since then, including reexamination of specimens collected during sets in the years 1971-74, indicate that through 1978, a total of 22 sets have been observed on coastal spotted dolphins, out of a total 9,672 observed overall (about 0.2%).

The yellowfin tuna purse seine fishery was concentrated nearshore in the early 1960's, and many sets were made in the area probably occupied by both coastal and offshore spotted dolphins. Direct observations in the 1960's distinguishing these forms of the spotted dolphin are not available. Based on observations made in the 1970's where these forms were distinguished, however, it appears that the coastal form has never been significantly involved in this fishery. Since 1978, sighting data collected by scientific observers aboard tuna vessels have been edited, using consistent criteria of school size, body size, and coloration for distinguishing coastal and offshore spotted dolphins. In 1979, for example, within about 50 km of the coast there were 46 sightings of coastal spotted schools, 160 sightings of offshore spotted schools, and 25 sightings of spotted dolphin schools which could not be distinguished to form with the available data. These three school types were subsequently set on in 2, 73, and 6 instances, respectively. Even assuming that all schools not identified to form were coastal spotted dolphins, the proportion of sighted coastal spotted dolphin schools subsequently set on is much smaller than that of the offshore form (0.11 vs. 0.46, $P<0.001$). This differential selection exists even though the catch of yellowfin tuna in sets on coastal spotted dolphins has been approximately twice that on offshore spotted dolphins. If coastal spotted dolphins were a significant part of this fishery, one would expect their involvement in sets to be proportional to the rate at which they are encountered.

In addition, 18 of the 22 sets on coastal spotted dolphins occurred in 1973, and, except for one set, these were made by two vessels in the Gulf of Nicoya, a small area off the Costa Rican coast. Based on this information, I have assumed that the coastal spotted dolphin has been involved only rarely in this fishery.

Two spinner dolphin populations, referred to as the "eastern" and "whitebelly" forms, are involved in the yellowfin tuna purse seine fishery. A third form, termed the Costa Rican spinner, occurs near the coast from Mexico to Panama, but is not involved in the fishery. The eastern and whitebelly forms overlap broadly in range, with the whitebelly spinner dolphin generally occurring more seaward. The eastern form has been involved with this fishery since 1959, whereas the whitebelly spinner dolphin population apparently became increasingly involved as the fishery expanded seaward in the 1960's.

The whitebelly spinner and the offshore spotted forms have Southern Hemisphere populations (Perrin et al. 1979). These populations have been involved only recently with the yellowfin tuna purse seine fishery, as it has expanded southward, and are only lightly exploited. Data on reproductive condition of these southern populations are used as estimates of reproductive rates for unexploited or equilibrium populations.

1979 POPULATION SIZE ESTIMATES

Holt and Powers (1982) gave estimates of abundance based on aerial and research-vessel sighting surveys and data from scientific observers aboard fishing vessels. Estimates of the size, N_i, of the ith population in their survey area are based on the equation

$$N_i = P_t \, S_t \, D \, P_i \, A, \qquad (5)$$

where P_t denotes the proportion of dolphin schools containing dolphin of the genera *Stenella*, *Delphinus*, and *Lagenodelphis*; S_t, the mean size of these schools; D, the estimated density of all dolphin schools sighted; P_i, the fraction of schools containing dolphins of the ith population; and A, the area inhabited. This equation is applied to 1) a nearshore stratum, surveyed using both an airplane and research vessels, and 2) an offshore stratum, surveyed only by research vessels. The nearshore stratum extends seaward from the coastline about 800 km, and from lat. 22°N to 12°S. The offshore stratum extends from the outer edge of the nearshore stratum to the boundary of the dolphin range.

Approximate areas of the maximum historical range of the three dolphin populations are used for the area inhabited, A in Equation (5). These are estimates of the area enclosed by a smooth curve which includes most locations where dolphins of different species have been reported by both fishing vessels and research vessels, as described in Holt and Powers (1982).

While occasional sightings of dolphin schools have been reported outside these areas, the areas are overestimated in that "...at any point in time it is likely that each of the various dolphin species only occupies a portion of its historical range."[4] Overlap between coastal and offshore forms of spotted dolphin is not reflected in the population estimates given by Holt and Powers (1982). Due to the large differences in areas inhabited, however, adjustments to account for the unknown degree of overlap would increase the offshore spotted dolphin population estimate by 3% at most, which is insignificant for the general results being presented here.

The density estimate for the nearshore area is obtained from line transect theory applied to aerial survey sighting data. This follows earlier applications (Smith 1981), but with several improvements. For instance, the aircraft we used had superior downward visibility; right-angle distance from the aircraft trackline to the sighted dolphin schools was determined directly, either by electronic navigation equipment or visually for shorter distances, rather than being calculated from visual estimates of range and bearing; and the originally used negative-exponential sighting model was replaced with the superior Fourier series model (Burnham et al. 1980). The density estimate for the offshore area, which could not be surveyed by air, is obtained by comparing relative dolphin school sighting rates from research vessel surveys in nearshore and offshore areas with absolute density estimates from the nearshore area. The resulting density estimate of all dolphin schools of >15 animals in the nearshore area is about 3.6 schools/1,000 km^2, while the density estimate in the offshore area is about one-half that value.

The school size estimate is about 200 animals, based on visual estimates of the size of schools seen during the aerial survey. The accuracy of these visual estimates has been confirmed by counts of individual dolphins from aerial photographs, and the accuracy of the counts from these photographs has been confirmed by counts of dolphins released from a purse seine (Allen et al. 1980). This estimated school size also includes an adjustment for the tendency of larger schools to be more readily visible at greater distances from the aircraft, and hence to be overrepresented in the sample.

Allen et al. (1980) also demonstrated that accurate school size estimates could be made from ships. Although not used by Holt and Powers (1982), the mean school size estimated from research vessel sighting data was about 180, not significantly different from the value derived from aerial data described above. In contrast, the mean school size estimated from tuna vessel sighting data collected by scientific technicians was about 580, significantly higher ($P<0.001$) than the other two values. This difference implies either nonrandomness of the sample of dolphin schools encountered by the tuna vessels, or biases in the estimation techniques used by the technicians.

P_i for each of the 22 populations involved in the yellowfin tuna purse seine fishery can be estimated from data collected aboard either tuna vessels or research vessels. Fishing vessels encounter significantly more schools composed primarily of spotted and spinner dolphins than do research vessels. The reason for this difference is not known, but it is possible that fishing vessels encounter spotted and spinner dolpin schools more frequently than would be expected under random search because they are searching for tuna, which occur with these two schools more frequently than with other species of dolphins. Studies of the searching process of tuna fishing vessels are being conducted which should help resolve this question. Because the proportions P_i are different for unknown reasons, Holt and Powers (1982) gave several sets of estimates of total abundance, depending on the estimates of P_i from different combinations of the research vessel and tuna vessel data. Two sets of estimates are considered here (Table 1), one using research vessel data alone and the other using combined tuna vessel and research vessel data.

Aerial survey procedures used in the present population-size estimates are still being refined. For instance, a field study was completed in mid-

TABLE 1.—Population size estimates (thousands) at the beginning of 1979 for three populations of dolphins in the eastern tropical Pacific, using estimates of the species mix from research vessel data alone, and from combined tuna vessel data and research vessel data, with standard deviations in parentheses (Holt and Powers 1982).

Population	Research vessel data only	Fishing and research vessel data
Offshore spotted	1,682.0 (471.8)	2,775.0 (761.4)
Eastern spinner	292.7 (71.0)	292.9 (64.4)
Whitebelly spinner	216.0 (67.4)	380.4 (134.9)

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[4] Hammond, P. S. (editor). 1981. Report of the Workshop on Tuna-Dolphin Interactions, Managua, Nicaragua, April 1981, p. 5. IATTC Spec. Rep. 4, Inter-Am. Trop. Tuna Comm., c/o Scripps Inst. Oceanogr., La Jolla, CA 92093.

1980 to determine the effect of sea state and sun position on the visibility of dolphin schools directly on the trackline. Data from this experiment, which have not yet been completely analyzed, will be of use in the design of future surveys and in the evaluation of earlier surveys.

INCIDENTAL KILL ESTIMATES

Incidental kill (K_t) of dolphins in year t is estimated by multiplying the mean kill of dolphins per set in year t (KPS_t) by the total number of net sets involving dolphins made by the tuna fleet in year t ($NSETS_t$), as

$$K_t = KPS_t \; NSETS_t. \tag{6}$$

These estimates are obtained for each year with the data stratified by vessel fish-carrying capacity, amount of tuna caught in the net set, and geographic location of the set, following the general approach described by Lo et al. (1982).

Kill rate information is available from a limited set of tuna fishing trips in the 1960's and from a more extensive set in the 1970's collected by scientific observers placed aboard a large proportion of the U.S. fishing vessels. To illustrate the data, some mean kill rates, stratified by amount of tuna caught, are shown in Table 2. Higher kill rates are apparent in successful (>¼ ton tuna caught) than in unsuccessful (<¼ ton tuna caught) sets, as are marked declines in kill rates over time. Numbers of dolphin sets and fishing trips on which observations of numbers of dolphins killed were made are shown in Table 3.

Observations of the numbers of dolphins killed in the 1960's were made by both the crew and the scientists. Although few observations were made, there is no consistent difference between kill rates reported by both types of observers (59 and 52, respectively); this suggests the presence of a noncrew-member observer had no significant effect on the kill rate of dolphins in the 1960's.

TABLE 2.—Observed mean kill of dolphins per net set (KPS) by U.S. tuna purse seiners 1964-78, for successful and unsuccessful net sets, with sample sizes (N), from NMFS records.

	Successful sets (> ¼ t tuna)		Unsuccessful sets (< ¼ t tuna)	
Year	KPS	N	KPS	N
1964-72	55.7	343	7.9	25
1973	22.6	576	0.6	130
1974	15.7	753	2.4	261
1975	18.9	778	2.5	169
1976	16.1	627	5.7	126
1977	3.4	2,706	0.9	495
1978	4.2	1,434	3.9	249

All data on kill rates of dolphins for the period 1971-78 were collected by noncrew-member scientists, precluding a direct comparison of kill rates between fishing trips with (observed) and without (unobserved) scientific observers for this period. Croom,[5] however, reported dolphin kill rates on a fishing trip in 1979 with no scientific observer on board; his kill rates were about 4 times higher than the average rate in 1979 for scientist-observed trips and were approximately 20 times higher than on previous and succeeding observed fishing trips by the same vessel and captain. This difference in mean kill rates was due to the significantly lower proportion of sets with few dolphins killed on Croom's trip than on the scientist-observed trips. For instance, the proportion of sets with zero dolphins killed was 0.23 on Croom's trip with 0.76 for observed trips.

Although limited information is available, it appears that kill rates on some unobserved vessels were higher in the late 1970's, and that this could result in the observed kill rates being lower than the actual rates. If there has been an "observer effect," it most likely occurred in the late 1970's, because regulations were adopted in the United States in 1976 requiring the use of certain dolphin-release procedures, and because scientific observers were then used to collect regulation compliance information. If kill estimates for the last few years were revised with this in mind, it would only slightly affect the calculations presented here, since the large number of animals killed through 1975 tends to dominate in Equation (2). However, such revisions to the kill estimates could markedly change our perception of the current rate of change of these populations.

In addition to the known direct kill of dolphins in the fishery, research has been conducted to estimate both the number of dolphins injured and released alive from the purse seines, and the possible number of dolphins which, while not exhibiting injuries, die or suffer reduced viability from stress of capture and handling in the purse seining operation. Observations of the number of injured dolphins have been made aboard tuna vessels since 1975; estimates of the number injured fluctuate around 4.8% of the number killed directly, ranging from 3 to 7%. The problem of stress-induced mortality or debility was explored in a workshop of experts on large mammal physiology and pathology, and research plans to approach this problem were developed.[6] Subsequently one aspect of this problem was examined with dolphin specimens collected aboard tuna vessels.[7] Reproductive tracts were examined for evidence of spontaneous abortion, and muscle tissue for myopathy; no evidence of either was found. No estimates of the magnitude of such effects have been made, and currently no research is underway to investigate stress-induced mortality. As a conservative measure, given our limited knowledge, I assume in the estimates of total dolphin mortality given here that all of the injured dolphins subsequently die of their injuries. Thus estimates of total kill of dolphins are the sum of the estimated numbers killed directly and the numbers injured.

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[5] Croom, M. M. 1980. The tuna-porpoise problem: Management aspects of a fishery. M.S. Internship Rep., Marine Resour. Manage. Program, Oreg. State Univ., Corvallis, 41 p.

Numbers of net sets made by the tuna purse seine fleet have been recorded by the Inter-American Tropical Tuna Commission (IATTC) from logbooks kept by the fishermen (Table 3). In the logbooks the type of each net set may be recorded, along with tuna catch, location, and other information. The three major types of sets are 1) those known to involve dolphins, 2) those known not to involve dolphins, and 3) those for which the data indicate neither the presence nor absence of dolphins. Types of sets not involving dolphins include "floating object sets" (e.g., a rope, board, log, etc.), a "school fish set" (i.e., a net set on tuna sighted at or near the surface), and a "porpoise set." The logbook data are incomplete, however, because some members of the fleet do not report and because, in some cases, only limited information was recorded by the fishermen. The logbook coverage rate, however, is high.

The data in columns *D*, *N*, and *U* in Table 3 have only recently become available, and analyses are proceeding to use this information directly to estimate the total number of sets made on dolphins. Preliminary results for the total numbers of sets for each year[8] are similar to those given in column *E* of Table 3, but the results are not yet available in the stratified form needed to estimate numbers killed, described below. Earlier estimates of the total number of sets made on dolphins (column *U* of Table 3) were obtained indirectly for the years prior to 1970, based on the catches of tuna, and include an adjustment for nonreported sets.

TABLE 3.—Number of tuna purse seine sets, 1959-78, (*D*) known to have been made on dolphins in the eastern tropical Pacific, (*N*) known not to have been made on dolphins, and (*U*) unknown if made on dolphins (IATTC text footnote 8), with (*E*) estimates of the total number of sets made on dolphins (Smith text footnote 3). Also shown are the numbers of observed fishing trips and purse seine sets on porpoise from NMFS records.

	Sets made				Sets observed	Trips observed
Year	*D*	*N*	*U*	*E*		
1959	132	759	2,985	1,037	0	0
1960	1,644	1,256	7,390	5,696	0	0
1961	3,617	3,825	8,694	8,247	0	0
1962	2,886	8,830	4,337	4,060	0	0
1963	3,290	9,266	6,322	4,687	0	0
1964	5,933	7,681	4,745	8,090	67	2
1965	6,172	7,176	5,631	7,981	0	0
1966	5,443	7,001	5,247	7,250	28	1
1967	3,510	10,018	3,594	4,478	0	0
1968	3,833	8,988	1,642	4,271	15	1
1969	7,664	6,552	2,055	8,678	0	0
1970	7,912	9,692	1,664	8,552	0	0
1971	4,816	10,728	3,404	5,039	78	5
1972	8,193	4,682	3,514	9,036	272	12
1973	8,686	9,463	3,672	9,998	752	22
1974	7,955	11,669	4,835	8,539	1,120	36
1975	8,172	13,396	4,902	8,951	1,049	31
1976	7,481	17,789	5,184	7,910	1,295	45
1977	7,485	15,005	7,643	9,757	3,335	94
1978	5,174	21,527	5,639	5,910	1,771	102

For the Period 1959-72

Estimating the annual rate of dolphin kill during the period 1959-72 is difficult because observations were few, especially in the early part of the period; consequently, extrapolation of information on kill rates is necessary. One effect on rate of kill is the development and improvement of the "backdown" dolphin-release procedure (Coe and Sousa 1972; Barham et al. 1977), by which the vessel moves in reverse during a short portion of the purse seine retrieval, thereby pulling the net out from under the dolphins. Barham et al. (1977) reported that the "backdown" dolphin-release procedure was developed aboard one vessel in 1959 and 1960, and transferred to a second vessel in 1961. Subsequently, the use of the procedure expanded rapidly within the fleet, although full use was not evident even by 1964. Comparing kill rates with and without "backdown" is complicated however, because the effectiveness of the release procedure has increased over time.

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[6] Stuntz, W. E., and T. B. Shay. 1979. Report on capture stress workshop, La Jolla, California, May 1979. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-79-28, 24 p.

[7] Cowan, D., and W. Walker. 1979. Disease factors in *Stenella attenuata* and *Stenella longirostris* taken in the eastern tropical Pacific yellowfin tuna purse seine fishery. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-79-32, 21 p.

[8] Inter-American Tropical Tuna Commission. 1981. Tuna-dolphin investigations. Background paper 6, prepared for the 39th meeting of the IATTC, Paris, October 1981. Inter-Am. Trop. Tuna Comm., c/o Scripps Inst. Oceanogr., La Jolla, CA 92093, 17 p.

No information is available on kill rates from non-U.S. vessels during 1959-72, but the non-U.S. fleet was small. There is little reason to suspect that these kill rates were different, because fishermen of both fleets were still learning how to use purse seine gear for catching tuna in association with dolphins and how to release the caught dolphins.

The available kill rate data for this period were stratified, for use in Equation (6), by amount of tuna caught, size of the vessel, and frequency of use of the "backdown" procedure. The data were pooled across the years 1964-72 and extrapolated back to the years 1959-63 when no kill rate data were collected. These stratified kill rates were multiplied by the number of sets made on dolphins in each stratum to estimate the total number of dolphins, of all populations, killed directly in this fishery.

Estimating proportions of the total kill of dolphins from each population for this period is difficult because the yellowfin tuna purse seining was expanding westward and because data on the species of dolphins observed killed are available only for 1971 and 1972. Prior to 1969 this fishery operated shoreward of the range of the whitebelly spinner dolphin, primarily within the range of the eastern spinner and offshore spotted dolphins. The total kill estimates are prorated to population for the years 1959-72, based on observed proportions in the 1971-72 data of 70, 23, and 3% for offshore spotted, eastern spinner, and whitebelly spinner dolphins, respectively. The other 4% consisted of several species, primarily common dolphins, *Delphinus delphis*, which are not considered in this study. Although the tuna purse seine fishery was expanding seaward throughout the 1960's toward the range of the whitebelly spinner dolphin, a major seaward shift occurred in 1969. Lacking detailed data, I assume this year to be the first significant involvement of the whitebelly population.

Some additional data on the species of dolphins involved in each set has recently become available from the IATTC, suggesting a declining proportion of sets involving spinner dolphins and an increasing proportion involving spotted dolphins throughout the 1960's. Preliminary examination of these data indicates that the overall proportions of sets involving each species are not greatly different from the 1971-72 observer data. Direct use of these new data will involve making a number of assumptions about species-specific kill rates.

Using the above proportions based on the 1971-72 data and increasing the estimates of total number killed by 4.8% to account for those dolphins possibly dying of injuries, I estimated the total numbers of dolphins killed, by population (Table 4). These are revisions of estimates used by the 1979 workshop (footnote 3).

TABLE 4.—Estimates of numbers (in thousands) of dolphins killed by all fleets in the eastern tropical Pacific, 1959-78, for three populations of dolphins (Smith text footnote 3).

Year	Offshore spotted	Eastern spinner	Whitebelly spinner
1959	71	27	0
1960	357	133	0
1961	402	150	0
1962	167	62	0
1963	183	69	0
1964	306	115	0
1965	337	126	0
1966	306	115	0
1967	206	77	0
1968	178	67	0
1969	365	122	15
1970	355	118	14
1971	176	59	7
1972	288	96	12
1973	131	32	33
1974	95	26	47
1975	105	45	34
1976	47	9	20
1977	22	5	5
1978	19	2	4

For the Period 1973-80

Substantially more data exist on kill rates for the period 1973-78 than for the period 1959-72. The 1973-78 data are more reliable because they were collected by NMFS employees trained specifically for obtaining kill information. Starting in 1974 fishing trips were randomly selected for observation to obtain a representative sample. Greater cooperation by the fishing fleet resulted in an increasing proportion of selected trips actually observed from 1974 to 1976. However, it was not until 1976 that fishing trips begun after July were sampled. In the early 1970's fishing tended to occur farther offshore later in the year; because kill rates are generally higher in the offshore areas, the failure to collect data from late-season trips probably resulted in an underestimate of actual dolphin kill rates in those years. This problem is partially accounted for by stratifying the data by area. The species composition of the kill was also recorded, allowing direct estimates of total kill of dolphins, from Equation (6), for each population.

The number of dolphins killed per set from 1973 to 1976 for successful and unsuccessful sets was about 18 and 3, respectively, a decrease from the 1964-72 levels of 56 and 8. The number killed in successful and unsuccessful sets in 1977 and 1978 was again lower, about 4 and 2, respectively (Table 2). These decreases occurred as U.S. regulations were developed and eventually implemented, and as methods for more effective use of backdown and other dolphin-release procedures were developed and used. The decreases in kill rates were apparently due, at least in part, to wider adoption of procedures for dolphin release.

The non-U.S. tuna purse seine fleet increased markedly during this period. First observations of the kill rate for this fleet were in 1979, which showed that the rate was very similar to that of the U.S. fleet (Allen and Goldsmith 1981). Given this similarity in 1979, it is reasonable to assume that during the earlier part of the 1970's the non-U.S. kill rate declined, as did the U.S. kill rate (Table 2), as dolphin-release technology developed by the U.S. fleet became known. If such a decline in the non-U.S. kill rate occurred, however, it would probably have been somewhat slower than that for the U.S. fleet, because of lack of legal pressure to reduce the incidental kill and time lags in technology transfer. Following the procedure developed by the 1979 workshop (footnote 3), I estimated the non-U.S. kill by assuming 1) the same kill rate in 1971-72 for the non-U.S. fleet as that observed aboard U.S. vessels in those years; 2) the same kill rate in 1973 for the non-U.S. fleet as that of the U.S. fleet in 1975; and 3) a linear convergence of the two rates toward the 1979 U.S. rate. Estimates of numbers of dolphins killed by non-U.S. vessels obtained under these assumptions are used here. However, additional study is needed, especially since the recorded kill rate for the non-U.S. fleet in 1980 was somewhat higher than that for the U.S. fleet (Allen and Goldsmith 1982).

These kill rates, stratified by vessel size, amount of tuna caught, and area fished, are used in Equation (6), along with the estimated number of sets on dolphins, to estimate total direct kill by population for each year. These estimates are then increased by 4.8% to account for dolphins assumed to die of their injuries (Table 4). The results in Table 4 are slight revisions of the estimates used by the 1979 workshop (footnote 3).

NET RECRUITMENT RATE ESTIMATES

Maximum net recruitment rate (R_m) is required to estimate historical abundance. This is calculated as the difference between gross production of calves and the natural mortality rate, assuming that natural mortality does not change, when a population is reduced substantially below its equilibrium level.

Gross Reproductive Rates

Gross recruitment rates can be estimated as the product of the female fraction of the population, the mature female fraction, and the annual pregnancy rates. Estimates of these parameters are given in Table 5, based on samples of dolphins collected by scientific observers aboard tuna vessels from 1973 to 1978. Two methods were used to estimate the annual pregnancy rate: The first method (I) is the observed proportion of pregnant females in the population divided by the gestation period; the second method (II) is similar, but uses additional information on frequency of nursing calves in the samples from each net set (Perrin et al. 1977a, b, c).

There are known sampling biases in these data for spotted dolphin because of the fishing process, partly accounted for by using data for spotted dolphin recruitment rates from only those sets where more than 40 dolphins were killed. In addition, the observed fraction of the mature, pregnant female dolphins has varied among years, with a general decline in offshore spotted dolphin and a large degree of variability in eastern spinner dolphin.

Age-specific effects are not accounted for in the analyses so far, however, particularly the

TABLE 5.—Proportion of sampled dolphins (female and mature) of three populations and estimates of annual pregnancy rate (P) and gross reproductive rate (G), using two methods.[1] See text for details.

			Annual production			
	Proportion		Method I		Method II	
Population	Female	Mature	P	G	P	G
Offshore spotted	0.56	0.56	0.38	0.119	0.32	0.100
Eastern spinner	0.51	0.43	0.34	0.075	0.45	0.099
Whitebelly spinner	0.51	0.52	0.36	0.096	0.33	0.088

[1] Henderson, J. R., W. F. Perrin, and R. B. Miller. 1980. Rates of gross annual production in dolphin populations (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific, 1973-1978. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-80-02, 51 p.

lower pregnancy rate that probably occurs in older animals. New methods are being developed for age determination, and an effort is being made to apply these methods to age the samples of dolphins. With accurate data on age of animals, a more detailed examination of sampling biases will be undertaken.

Natural Mortality Rates

No direct estimates of natural mortality rates exist for the eastern Pacific dolphin populations, as might be obtained from tagging data or from a sampled age structure. Ohsumi (1979) presented a statistical relationship between natural mortality rate and body length for cetaceans, from which can be derived an annual, natural mortality rate of around 0.14 for the eastern Pacific dolphin populations. However, this estimate is obtained by extrapolating the relationship outside the range of his data, and consequently is unreliable.

Another method of estimating natural mortality rate is from information on gross reproductive rate for a population in equilibrium with its environment, assuming natural mortality does not change with population size. This approach was used in the 1976 workshop (footnote 2). An estimate of gross reproductive rate of 0.09 (Kasuya et al. 1974) for a population off Japan, thought to be lightly exploited, was used as the natural mortality rate estimate for the eastern tropical Pacific populations. It now appears that the population off Japan had, in fact, been exploited to a greater degree than was thought, and that there is segregation of prepubertal dolphins into separate schools (footnote 3, p. 41). The assumption, consequently, of a natural mortality rate of 0.09 is probably not valid.

In the 1979 workshop (footnote 3), estimates of the gross reproductive rate of lightly exploited Southern Hemisphere populations of spotted and spinner dolphins in the eastern tropical Pacific were used as estimates of natural mortality rates. These rates were 0.098 and 0.067 for spotted and spinner dolphins, respectively.

Net Rates

Net recruitment rates for the offshore spotted, eastern spinner, and whitebelly spinner dolphin populations can be estimated as the differences between the gross reproductive rate estimates, listed in Table 5, and the corresponding natural mortality rate estimates given above. Using method I estimates of pregnancy rates, one obtains estimated net reproductive rates of 0.021, 0.008, and 0.029 for these three populations, respectively. Using method II estimates of pregnancy rates, one obtains estimates of 0.002, 0.032, and 0.021, respectively. These highly variable estimates are unsatisfactory, because they are based on data with known sample biases, and they differ among populations in unexpected ways. In particular, it is not expected that the net reproductive rate of the whitebelly spinner dolphin, which has been relatively less exploited, should be higher than that of the more heavily exploited eastern spinner dolphin population.

Due to these uncertainties, specific point estimates were not obtained by the 1979 workshop participants. Rather, a range of values from 0.0 to 0.04 were considered equally likely, given the available information. The lower value of 0.0 was selected by the 1979 workshop to reflect uncertainties about unexpected changes in some reproductive rates, and the small magnitude of the estimates of net reproductive rates. This range compares with the estimates from the 1976 workshop of 0.02-0.06, with a midpoint estimate of 0.04. Although higher rates of increase of cetacean populations have been reported, contrary to the conclusions in the 1979 workshop report, there are no reliable estimates of rates of increase for dolphin populations which can be used with confidence. Pending better information, the range of estimates considered in the two workshops will be used here, recognizing that higher rates may be possible.

Rate Dependent on Population Size

The evidence on which to base an estimate of the value of Z in Equation (3) for dolphin populations is limited. Fowler (1981) argued that for large, long-lived mammals, Z is greater than unity. He based this conclusion on a review of empirical data, primarily from terrestrial populations, and on an analysis of the demographic constraints which come with long life and extended parental care. McCullough (footnote 3, p. 8) gave preliminary estimates of maximum net productivity level (*MNPL*), and hence Z, for four large terrestrial mammal populations. His estimates agree with Fowler's conclusions that Z is greater than unity, and that later reproducing animals would have higher values of Z.

The 1976 workshop (footnote 2) concluded that the available information implies *MNPL* is within the range of 50-70% of the equilibrium population size, corresponding to values of Z from 1 to 5.1. The 1979 workshop recognized that "There had been a shift of scientific opinion in recent years [since 1976] towards accepting the idea that relative net productivity in mammals, especially large, K-selected species, is a non-linear function of population size," (footnote 3, p. 7) and concluded that *MNPL* for these dolphin populations is probably in the range of 65-80% of the equilibrium population size (Z from 3.5 to 11.5). I consider the values for *MNPL* of 50-80% (Z from 1 to 11.5) of equilibrium population size in order to explore the sensitivity of the calculations to this uncertainty.

HISTORICAL TRENDS IN ABUNDANCE

Estimates of population sizes prior to 1979 from Equations (2) and (3) for each population are shown in Table 6. Values are given using 1) two different estimates of present (1979) abundance (from combined research vessel and fishing vessel data, and from research vessel data alone), and 2) the parameters $MNPL = 65\%$ and $R_m = 0.03$. For this range of parameter values, the offshore spotted dolphin population in 1959 was between about 4,800,000 and 5,600,000 animals. The eastern spinner dolphin population in 1959 numbered about 1,500,000, while the white-

TABLE 6.—Estimates of population size (in thousands) of offshore spotted, eastern spinner, and whitebelly spinner dolphins from 1979 back to 1959, using Equations (2) and (3) and parameters $MNPL = 65\%$ and $R_m = 0.03$. 1979 estimates are based on species proportions from (*FR*) combined research vessel and fishing vessel data and (*R*) research vessel data alone.

	Offshore spotted		Eastern spinner	Whitebelly spinner	
Year	*FR*	*R*	*FR* = *R*	*FR*	*R*
1979	2,775	1,682	293	380	216
1978	2,719	1,653	287	376	215
1977	2,668	1,628	283	373	214
1976	2,673	1,629	284	386	229
1975	2,675	1,686	320	434	258
1974	2,679	1,732	336	456	301
1973	2,754	1,824	358	486	331
1972	2,967	2,046	443	494	340
1971	3,064	2,164	488	499	345
1970	3,340	2,457	591	512	358
1969	3,264	2,756	695	527	373
1968	3,720	2,865	742	527	373
1967	3,844	3,001	799	527	373
1966	4,071	3,239	893	527	373
1965	4,335	3,520	998	527	373
1964	4,574	3,754	1,092	527	373
1963	4,695	3,879	1,141	527	373
1962	4,803	3,991	1,185	527	373
1961	5,169	4,358	1,323	527	373
1960	5,519	4,708	1,454	527	373
1959	5,590	4,779	1,481	527	373

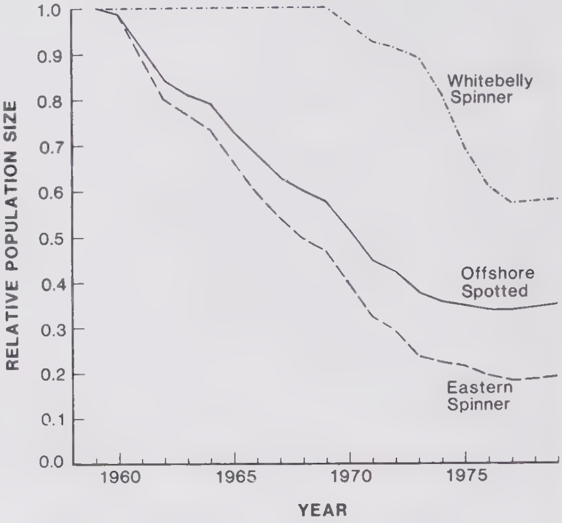

FIGURE 1.—Relative population sizes of whitebelly spinner, offshore spotted, and eastern spinner dolphins, 1959-79, using population estimates based on species proportions from combined research and fishing vessel data, and assuming $R_m = 0.03$ and $MNPL = 65\%$ of equilibrium abundance. Population sizes are relative to estimated population sizes in 1959.

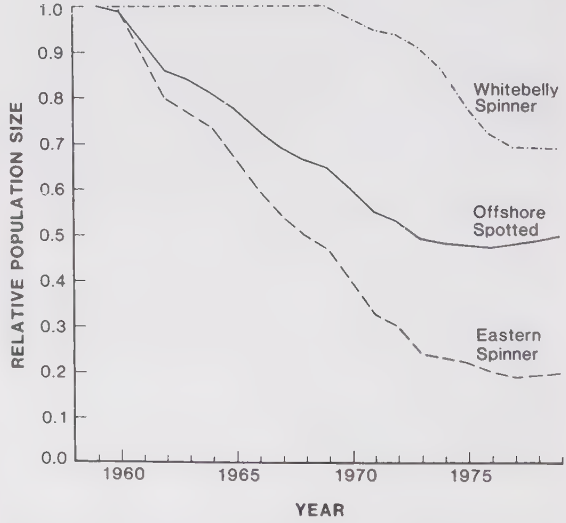

FIGURE 2.—Relative population sizes of whitebelly spinner, offshore spotted, and eastern spinner dolphins, 1959-79, using population estimates based on species proportions from research vessel data alone, and assuming $R_m = 0.03$ and $MNPL = 65\%$ of equilibrium abundance. Population sizes are relative to estimated sizes in 1959.

belly spinner dolphin population in 1969 numbered between 400,000 and 500,000. The offshore spotted and eastern spinner dolphin populations declined rapidly in the 1960's and early 1970's in the face of kills which were, for example, on the order of 7-12% of the 1965 population sizes. The whitebelly spinner dolphin population declined most rapidly in 1974 when the kill was between 11 and 16% of its population size.

These estimates of absolute population sizes are shown in Figures 1 and 2 relative to the equilibrium population size (N_t/N_p), so that the trend in abundance of these populations can be examined. For all of the parameter values considered, these dolphin populations have declined substantially relative to their pre-exploitation sizes.

The ratio of 1979 to pre-exploitation population sizes for different values of R_m and *MNPL* (and hence Z) shows the sensitivity of the calculations to changes in parameter estimates (Table 7; Figs. 3, 4). The value of *MNPL* when R_m is zero is not meaningful, as the estimate of pre-exploitation population size (Equation (2)) collapses to the sum of the present population size estimate and the total numbers killed over all years. This is reflected in Figures 3 and 4 in the convergence of the lines when R_m is zero.

TABLE 7.—Estimates of 1979 relative population sizes of offshore spotted, eastern spinner, and whitebelly spinner dolphin populations, using two estimates which differ in species proportions from (*FR*) combined fishing and research vessel data and from (*R*) research vessel data alone, for ranges of maximum net recruitment rate (R_m) and maximum net productivity level (*MNPL*).

		Offshore spotted		Eastern spinner	Whitebelly spinner	
R_m	*MNPL* (%)	*FR*	*R*	*FR* = *R*	*FR*	*R*
0.00	—	0.40	0.29	0.17	0.66	0.53
0.03	50	0.45	0.32	0.18	0.69	0.55
	65	0.50	0.35	0.20	0.72	0.58
	80	0.53	0.37	0.21	0.77	0.61
0.06	50	0.49	0.35	0.20	0.71	0.57
	65	0.60	0.42	0.23	0.78	0.63
	80	0.68	0.47	0.25	0.86	0.69

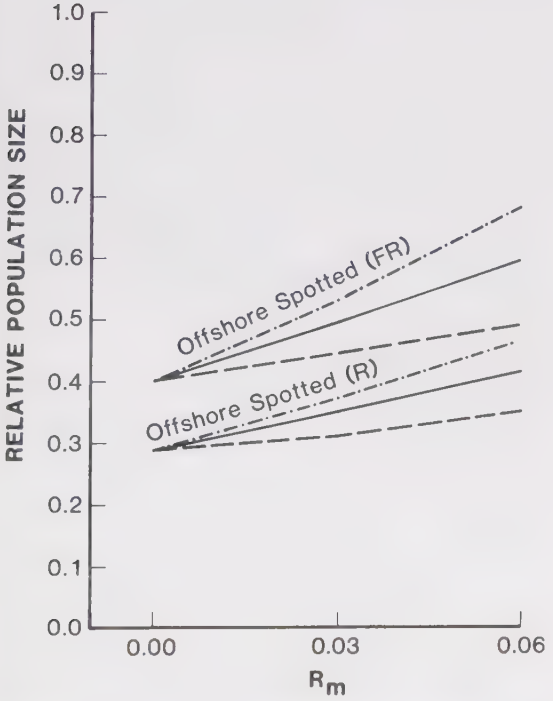

FIGURE 3.—Population size of offshore spotted dolphins in 1979 relative to 1959 (N_{79}/N_{59}) as a function of maximum recruitment rate (R_m = 0, 3, 6%) using two current population estimates which differ in species proportions from (*FR*) combined fishing and research vessel data and from (*R*) research vessel data alone. *MNPL* values of 50% (dashed lines), 65% (solid lines), and 80% (dot-dashed lines) are shown.

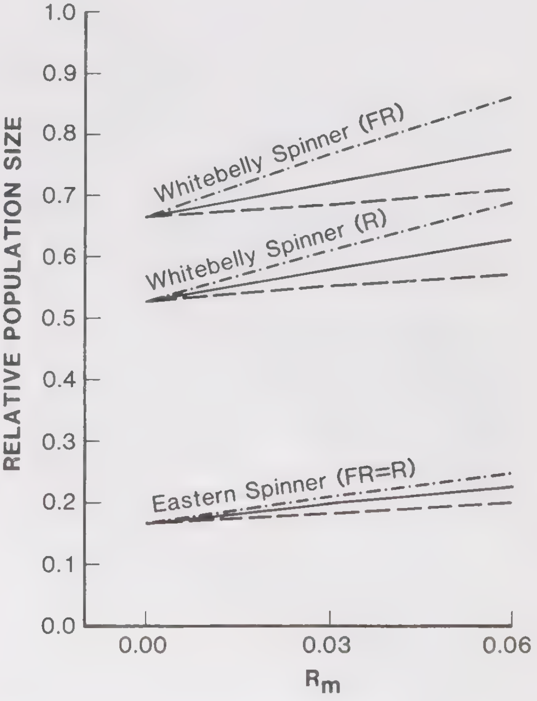

FIGURE 4.—Population sizes of eastern spinner and whitebelly spinner dolphins in 1979 relative to 1959 (N_{79}/N_{59}) as a function of maximum recruitment rate (R_m = 0, 3, 6%) using two current population estimates which differ in species proportions from (*FR*) combined fishing and research vessel data and from (*R*) research vessel data alone. *MNPL* values of 50% (dashed lines), 65% (solid lines), and 80% (dot-dashed lines) are shown.

DISCUSSION AND CONCLUSIONS

The three populations of dolphins involved with the yellowfin tuna purse seine fleet in the eastern tropical Pacific have declined since 1959 and the decline was not arrested until recently (Figs. 1, 2). Assuming the historical kill level, and the central values for R_m and *MNPL*, the whitebelly spinner dolphin population has declined to between 58 and 72% of its pre-exploitation levels; the offshore spotted dolphin population has declined to between 35 and 50% of its pre-exploitation size; and the eastern spinner dolphin population has declined to around 20% of its pre-exploitation size.

Examination of Figures 3 and 4 shows that the numerical values of the estimates of relative abundance in 1979 for offshore spotted dolphin and whitebelly spinner dolphin are relatively more sensitive to changes in the maximum net recruitment rate and the maximum net productivity level parameters than are the estimates for the eastern spinner dolphin. Also, the sensitivity of these calculations to the maximum net productivity level increases markedly as the value of the maximum net recruitment level increases. The sensitivity (in percent change) in the ratio of present to pre-exploitation abundance, however, is largest for the offshore spotted dolphin and least for the whitebelly spinner dolphin. This is due in part to the shorter time span over which the whitebelly spinner dolphin has been exploited, and in part to the lower $\frac{N_t}{N_p}$ ratio for the eastern spinner dolphin ratio, which makes smaller differences result in a larger percentage.

Although there are a number of uncertainties about specific parameter estimates used in these calculations, the general declines in abundance change relatively little over the ranges of parameter estimates explored. For example, rather rapid declines in the 1960's, followed by decreasing rates of decline in the 1970's, are evident for all parameter values considered. Specific aspects of these declines in abundance, however, depend to a greater degree on the actual parameter values. For example, the estimated changes in population sizes from 1975 to 1978 vary with the specific values of maximum net recruitment rate, while the estimated changes in population sizes in the 1960's are relatively insensitive to this parameter.

In order to improve our estimates of reproductive and mortality rates, a complete review of vital rates for these dolphin populations and for cetaceans in general should be carried out. Several approaches to this problem have been identified, including a detailed review of the eastern tropical Pacific dolphin data and of the existing data for other cetacean populations. Given the gaps in our knowledge of cetacean reproductive processes, analyses of alternate mathematical models of such processes will be fruitful.

Although improvements in estimates of abundance and kill levels are needed, these areas are generally much better understood than the recruitment process. Population-size estimation techniques are still being improved upon; current emphasis is on testing the assumptions needed in applying line transect theory to aerial sighting survey data and in estimating dolphin school size. Future work will emphasize improved shipboard sighting methodology for possible application of line transect theory.

Marked improvements in the estimates of numbers of dolphins killed are not anticipated; key areas needing additional information are the kill rates both in the non-U.S. fleet and on unobserved fishing trips. Neither of these areas is readily amenable to study, although further analysis of the kill rates on unobserved trips may provide some basis for exploring this uncertainty. The possible levels of indirect mortality or debility due to the stress of chase and capture are also of concern. Because of the large numbers of dolphins captured and released each year, even very low rates of indirect mortality could have a significant effect on the population.

ACKNOWLEDGMENTS

This assessment of the status of the dolphin populations is built on data collected by many individuals. The collection of these data has been made possible in large measure by the cooperation of the U.S. tuna fishing fleet. In addition, many individuals have contributed to the analysis of the data, including National Marine Fisheries Service staff and numerous scientists from various organizations. It is not possible to acknowledge the contributions of specific individuals to information presented here because of the large numbers of people who have been involved, but without their efforts the present analysis would not be possible. I also wish to acknowledge the very helpful reviews of an earlier draft of this paper by Douglas Chapman, John Gulland, Linda Jones, and Jeff Breiwick.

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Abundance of Pelagic Resources Off California 1963-78, as Measured by an Airborne Fish Monitoring Program

JAMES L. SQUIRE, JR.

ABSTRACT

From September 1962 through December 1978 commercial aerial fish-spotter pilots operating off southern and central California and northern Mexico, maintained a flight log indicating the geographical areas searched and an estimate of the quantity of pelagic species observed. These flight logs were analyzed for quantities of the various species observed per block area (10′ longitude by 10′ latitude area). Flights were recorded as surveying all or a portion of 164,753 block areas. A total of 110,375 block areas were surveyed during the day and 54,378 during night operations. An annual index of apparent abundance (arbitrary values) was computed for each of the major species observed, both for day and night aerial observations from selected geographical areas, and for total observations. The index value computed is not directly comparable between species.

During the period of the survey, the apparent abundance index for Pacific sardine, *Sardinops sagax caerulea*, declined from 1.03 in 1964 to 0.00 in 1974, and no significant schools have been observed by aerial surveys since. The northern anchovy, *Engraulis mordax*, night apparent abundance index remained relatively constant from 1963 to 1969 (2.99-4.35), increased substantially in 1973 to 14.99, then declined by 1978 to a level (1.91) near that observed in 1963-69. The day index for Pacific bonito, *Sarda chiliensis*, declined to a low level in 1968-69 (0.43-0.26), increased in 1972 to 1.11 (a year of above average sea surface temperature), and in subsequent years declined again to a low level (±0.1). Pacific mackerel, *Scomber japonicus*, population biomass was apparently low in 1962 at the start of the surveys, and continued to decline to very low night abundance levels during 1967-75 (undefined range of 0.00 to 0.03). In 1976 a small increase in the overall apparent index was recorded. By 1977 the night index had increased to 2.62, and in 1978 it again increased to a high level of 7.46. Jack mackerel, *Trachurus symmetricus*, showed a declining abundance index value during 1969-75 (0.66-0.40). A small increase in the night index apparent abundance was noted in 1976, and in 1977 the night index increased to 2.77. In 1978 it then increased about 1.5 times to a record high of 4.20.

Downward trends in apparent abundance indexes were noted 1 to 2 yr in advance of declines in the commercial catches for northern anchovy and Pacific bonito. Limitations of collected nonrandom data and variations in sightings and school size estimation between pilots are discussed. The apparent abundance indexes obtained from aerial surveys are compared with measures from larval and acoustical surveys.

A rank correlation analysis was made to measure the agreement between independent estimates of northern anchovy spawning biomass, larval index, and aerial index. Significant correlations were found for the aerial and acoustical survey indices of 1972-78 for the northern anchovy ($r_s = 0.810$, significant at the 0.05 level). During this period only three larval surveys were conducted, insufficient to calculate correlation. For earlier data, 1962-66 and 1968-69, larval vs. aerial index gave a poor correlation (+0.30). A significant correlation was evident for Pacific mackerel aerial index vs. spawning biomass index (r_s – 1.00).

INTRODUCTION

The Southwest Fisheries Center, National Marine Fisheries Service (NMFS), initiated an aerial pelagic fish monitoring program in 1962 with the cooperation of fish-spotter pilots active in locating fish for the central and southern California commercial purse seine fishery. The program utilized the services of the aerial fish-spotter pilot as a spin-off from their major occupation. The objective of the monitoring program was to measure and evaluate the apparent abundance of pelagic near-surface schooling fishes.

It was originally hypothesized that basic sighting data for the various species—tonnage estimates, or numbers of schools and their individual tonnage estimates, compared with search effort—would provide a measure of the relative apparent abundance of each species within a fishing area. Such information would be useful in assessment of the available stocks. Since sighting information from the spotter pilots is used as an aid in fishing, the efficiency of the pilot in locating schools and sometimes directing the setting of the purse seine has affected the catch per effort of the purse seiner. Therefore, aerial spotter data may be more useful than fishing vessel records for detecting changes in abundance of intensively fished species. The aerial fish-spotter also records the abundance of pelagic species which may not currently be targeted upon by the fishery. Aerial survey data, therefore, can be particularly useful in evaluating underutilized pelagic near-surface schooling resources.

The first report on the results of the program (Squire 1972) reviewed trends in apparent abundance for data collected from 1962 through 1969. This review updates these data through 1978 using the same analytical methods. Since publication of the first review, considerable changes in the apparent abundance levels of some pelagic species has occurred. The species of interest to this program are all members of a complex, interacting coastal ecosystem, and these data may assist in better defining changes in abundance levels over time which occur within the coastal pelagic resources complex. For a definition of terms used such as abundance, apparent abundance, and relative apparent abundance, see Marr (1951)

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[1] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038

The fish species most commonly observed by the commercial fish-spotters while operating off central and southern California, and northern Baja California, Mexico, are the northern anchovy, *Engraulis mordax*; jack mackerel, *Trachurus symmetricus*; Pacific bonito, *Sarda chiliensis*; Pacific mackerel, *Scomber japonicus*; Pacific sardine, *Sardinops sagax caerulea*; and bluefin tuna, *Thunnus thynnus*. Other species such as Pacific barracuda, *Sphyraena argentea*, yellowtail, *Seriola lalandei*, white seabass, *Atractoscion nobilis*, and albacore, *Thunnus alalunga*, are observed by the pilots, and are sometimes caught by the commercial fleet with the aid of aerial spotters. Other animals such as the basking shark, *Cetorhinus maximus*, mammals (whales and porpoise), and invertebrates (squid—*Loligo opalescens*), have been observed and recorded. A total of 20 species of fish have been observed and recorded by the spotter pilots (Squire 1972).

METHODS

Commercial aerial fish-spotters have recorded flight tracks and fish school tonnage estimates for the program since the fall of 1962; 1963, however, was the first complete year of data. The pilots in the program are full-time professional commercial fish-spotter pilots. Participating pilots under contract were advised that all sightings of schooling fish were to be reported. A total of 15 pilots have participated in the program. Observation quality has remained relatively stable since the pilots who have made the major contributions to the program have participated in it throughout its 16-yr period. There has been no attempt to intercalibrate the pilots. The only data gap in the program is for the second half of 1970 (July through December), when contracts for observation data were cancelled.

For a review of the methods and procedures for obtaining and processing the flight log observation data, and for results of the program for the period 1963-69, see Squire (1972). Caruso[2] described by details of computer coding of the aerial observations for future analysis. The general procedure for recording fish sighting observations on flight log charts has not changed from that described by Squire (1972). In 1974 flight log charts were added to cover the northwest coast of Baja California, Mexico. With the addition of charts for the area south of the United States-Mexico border, pilots recorded observation sighting data for summer flights in search of bluefin tuna. The borders of 10′ longitude × 10′ latitude "block areas" and associated "block numbers" were printed on the charts to expedite data coding. The "block areas" referred to are identical to the California Fish and Game statistical grid system. The area from Half Moon Bay, Calif., to Cedros Island, Baja California, Mexico, has six flight log charts. Divisions of this area into "block areas," which were later combined into larger grouped "zones" lettered A through T, are shown in Figure 1.

Pilots recorded their flight paths and school sightings on the appropriate charts. Aerial spotter data was analyzed by using summaries of the number of block areas entered into by the pilots as a measure of observation effort and tonnage estimates of fish.

Approximately 40,000 flight hours of observations were recorded. A total of 164,753 block areas or portions of block areas were surveyed: 110,375 (67%) during the day and 54,378 (33%) during the night (Table 1). A graph of each year's day, night, and total observation effort is given in Figure 2.

From 1962 to 1978, no natural changes in the survey area occurred that could be classed as atypical. However, one unusual event did occur that had a severe local impact and affected the observation of near-surface pelagic species. In late January 1969, a large release of crude oil occurred in the Santa Barbara Channel area. The oil release continued in varying quantities for some months afterward, and affected fishing and aerial fish-spotting operations in the eastern half of the Santa Barbara Channel and around the Channel Islands. Since this was an area where concentrations of anchovy, jack mackerel, and Pacific bonito were previously observed by the aerial spotters and fished by commercial seiners, the oil contamination resulted in a temporary cessation of fishing. During the months when the surface crude oil spill was a problem, however, frequent aerial surveys of the Santa Barbara Channel and Islands area were made by the Union Oil Company, using an aerial spotter pilot who was participating in the NMFS program. Data from these observations were recorded in the same format as the NMFS pelagic fish program and made available to the NMFS for analysis.

Flight log data represent a sample estimate of the apparent abundance of pelagic species schooling in the near-surface layers of the areas surveyed. The selection of flight tracks was nonrandom,

Table 1.—Observation effort off California for pelagic commercial fish (day/night) in units of block area overflights by zone.

Zone	1962-65	1966-69	1970-73	1974-78	Total
A	443/310	1,271/38	14/0	22/0	1,750/348
B	1,148/600	2,025/113	218/48	180/53	3,571/814
C	2,098/2,207	6,020/2,053	10,508/3,151	6,213/3,475	24,839/10,886
D	1,043/1,190	5,023/1,921	5,075/1,503	4,659/3,801	15,800/8,415
E	151/427	336/287	124/122	743/298	1,354/1,134
F	40/181	166/316	123/732	381/472	710/1,701
G	1,329/1,512	3,583/3,206	4,222/3,899	7,974/8,369	17,108/16,986
H	1,041/967	1,829/1,556	1,612/2,001	3,156/2,595	7,638/7,119
I	1,238/510	2,585/1,215	1,178/1,298	3,356/1,026	8,357/4,049
J	1,599/626	3,538/749	4,208/211	5,353/726	14,698/2,312
K	35/0	315/52	932/72	1,796/38	3,078/162
L	0/0	0/0	1,287/47	5,157/202	6,444/249
M	0/0	0/0	22/3	43/0	65/3
N	0/0	0/0	878/0	3,094/165	3,972/165
O	0/0	0/0	0/0	0/0	0/0
P	0/0	0/0	212/0	618/35	830/35
Q	0/0	0/0	0/0	0/0	0/0
R	0/0	0/0	0/0	161/0	161/0
					110,375/54,378

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[2] Caruso, J. 1979. Aerial marine resources monitoring system. Data Coding Manual. Admin. Rep. LJ-79-9, 99 p. Southwest Fisheries Center La Jolla Laboratory, NMFS, NOAA, La Jolla, CA 92038

being determined by past experience regarding the most likely locations for sighting schools of various species, real-time information from fishing boats and other spotter aircraft, and other recent experience. The species identification of the schools was determined during the day by physical characteristics such as shape or color of the fish or school, or by behavior of the fish. During the night, identification was made by the bioluminescent characteristics of the school's shape or its behavioral response to a flash of light. Information from fishing vessels was sometimes used in determining species composition, particularly where "mixed schools" were encountered.

A pilot's estimate of school tonnage is based on many years of observing school size, shape, depth, and quantity as determined by catching the fish observed. It is possible to estimate a school's vertical depth (distance from top of school to bottom) for schools of the larger pelagic species and small schools of such species as the northern anchovy. However, for large schools of the smaller forage species, the actual depth of the school usually cannot be determined from the air. Therefore, information from fishing vessels was frequently used since they could determine the school's vertical depth using an echosounder. The horizontal shape and area of the school could be estimated visually. Aerial spotter pilots are often paid on the basis of tonnage caught, so a close check on tonnage taken by the purse seiner is important to the pilot.

SIGHTINGS AND ABUNDANCE INDEX TRENDS BY SPECIES

Geographical Distribution of Fish School and School Group Sighting

Current and historical records, based on catch or fishing boat logbook data, give some indication of the location of catch, but only by "block area" (a 10′ longitude × 10′ latitude area), which measures about 8 × 10 nmi each at the latitude of southern California. A more detailed description of individual locations of the center of school or school group sightings as observed on each flight (day plus night) for the period 1962 through 1978 is given in Figures 4-61.

An illustration of how the center of sighting was determined is given in Figure 3. The dot on the chart is the geographical center of the sighting, representing one or more animals or schools observed in the area. On some charts having a high density of sightings, an overlap or masking may occur, particularly for anchovy.

Locations of centers of sightings are given for the northern anchovy (Figs. 4-11), Pacific sardine (Figs. 14-18), Pacific bonito (Figs. 20-27), Pacific mackerel (Figs. 30-36), jack mackerel (Figs. 38-45), bluefin tuna (Figs. 47-49), albacore tuna (Figs. 50 and 51), yellowtail (Figs. 52 and 53), Pacific barracuda (Figs. 54 and 55), white seabass (Figs. 56 and 57), basking shark (Figs. 58 and 59), and squid (Figs. 60 and 61).

A review of the sighting distribution charts is given in the following sections for those areas having the most sightings. In many instances the charts for north of Morro Bay and those below the United States-Mexico border are not shown because the observation effort was low, or the effort was not expended in areas where the species of interest would be commonly observed. For example, anchovy charts are not given for the Monterey Bay area because, although anchovies have frequently been observed in the area, the observation effort since the mid-1950's has been low. Most of the flight observation effort south of the United States-Mexico border has been offshore in search of bluefin tuna, and, as a result, nearshore areas commonly having schools of anchovies are rarely surveyed and are therefore not given.

During the survey period, the following total number of sightings of schools or school groups were made: northern anchovy, 8,720; Pacific sardine, 195; Pacific bonito, 3,873; Pacific mackerel, 1,273; jack mackeral, 3,233; bluefin tuna, 1,314; albacore tuna, 200; yellowtail, 94; Pacific barracuda, 138; white seabass, 70; and squid, 384. The observations of schools or school group for the major species observed represent a total tonnage sighted by day and night of 43,013,254 t of northern anchovy; Pacific sardine, 442,644 t; Pacific bonito, 442,644 t; Pacific mackerel 1,364,048 t; jack mackerel 1,869,256 t; and bluefin tuna, 507,366 t.

Apparent Abundance Index Trends

Day and night indices of apparent abundance for each zone and grouped zones have been calculated annually since 1963 for species of northern anchovy, Pacific bonito, jack mackerel, Pacific mackerel, Pacific sardine, Pacific barracuda, and yellowtail. Bluefin tuna indices have been calculated since 1974.

In calculating the index value, one of four arbitrary tonnage ranges for each species was assigned. These cover the range of observed tonnages that might be estimated to occur in any one block area. In order to provide a tonnage range value (x) the midpoint of each range was divided by 100 for the northern anchovy, a species that is observed in larger quantities compared with any others and by 10 for Pacific bonito, jack mackerel, Pacific mackerel, Pacific sardine, and bluefin tuna. The midpoint of the tonnage range for yellowtail and white seabass was not reduced. The range of observed tonnage and resulting x values are given in Table 2. The

Table 2.—Range of tonnage and tonnage range values (X). X is the index value based on the midpoint of the observed tonnage/100 (but not for barracuda or yellowtail).

Species	Observed tonnage	X
Anchovy	0-400	2
	401-1,000	7
	1,001-10,000	55
	10,001-20,000	150
Pacific bonito	0-50	2.5
	51-150	10
	151-1,000	57.5
	1,001-5,000	300
Jack mackerel	1-50	2.5
	51-300	17.5
	301-1,000	65.5
	1,001-2,000	150
Pacific mackerel	0-20	1
	21-100	6
	101-250	17.6
	251-500	37.5
Pacific sardine	0-100	5
	101-500	30
	501-2,000	125
	2,001-4,000	300
Bluefin tuna	0-50	2.5
	51-250	15
	251-1,000	62.5
	1,001-4,000	250
Pacific barracuda	0-10	5
	11-30	20
	31-80	55
	81-160	120
Yellowtail	0-5	2.5
	6-10	7.5
	11-30	20
	31-60	45

following formula was used to calculate annual indices of apparent abundance, day and night, by zone and by species:

$$\text{Index of apparent abundance} = \frac{\Sigma N_1X_1 + N_2X_2 + N_3X_3 + N_4X_4}{N}$$

where $N_{1,2,3,4}$ = number of block area flights in which the species occurred at value $X_{1,2,3,4}$,
$X_{1,2,3,4}$ = tonnage range values,
N_t = total number of block area flights in the zone during the year.

The index value, then, represents the relationship between the amount of fish observed (tonnage range value—x), divided by the amount of search effort (number of block area flights) conducted either during the night or during the day. Day and night indices of apparent abundance for each zone, and the annual average day/night indices of apparent abundance for all zones, are listed in Table 3. The boundaries of the zones were selected to outline important geographical areas where fish were commonly observed.

The index trends reviewed here are for the major commercial species of northern anchovy, Pacific sardine, Pacific bonito, Pacific mackerel, jack mackerel, and bluefin tuna. Apparent abundance trends for yellowtail and Pacific barracuda, species which are primarily targets of the recreational fishery, are given in Table 3 but are not reviewed here. During the survey period, sightings of these species were few, and have been much reduced in recent years, with a resultant decrease in indices.

An analysis of sightings by day or night and of tonnage observed (Squire 1972), indicated that the northern anchovy, Pacific mackerel, jack mackerel, and Pacific sardine were observed more frequently and in greater quantity during the night. Pacific bonito and bluefin tuna were observed in greater quantity in the day. The selection of the index that is most representative of the apparent abundance of each species is based on the 1972 study.

In the following sections, total effort and observations by year are shown in graphic displays of day/night index values and U. S. fishery catch trends during 1963-78 for each species, along with a review of areas of high sighting density during 1962-78.

Northern Anchovy

Morro Bay to San Nicolas Island.—1962-65, Fig. 4; 1966-69, Fig. 5; 1970-73, Fig. 6; and 1974-78, Fig. 7.

The sighting effort north of Pt. Conception was greatly reduced after the 1962-65 period. Anchovy schools were commonly observed off Morro Bay and Avila, the latter area being a location where schools were commonly observed. The Santa Barbara coast from Gaviota eastward, and into the eastern end of the Santa Barbara Channel, had a high level of anchovy sightings, with the major area of sighting located offshore between the cities of Santa Barbara and Ventura. In 1974-78, the center of sighting appeared to be slightly farther offshore between Santa Barbara and Ventura, but in 1978, the center of sighting appeared about equidistant between the two cities and much nearer shore than observed in previous years.

Pt. Hueneme to San Diego.—1962-65, Fig. 8; 1966-69, Fig. 9; 1970-73, Fig. 10; 1974-78, Fig. 11.

In 1962-65, anchovy sightings were evenly distributed between Pt. Hueneme and Dana Point, in the Catalina Channel, and about Catalina Island. Sightings were less frequent south of Dana Point to San Diego. From 1966 to 1969, the observations were centered in the Catalina Channel and numerous observations were also made off the coast from Long Beach to Newport Beach.

From 1970 to 1973, the major observation areas were again near the center of the Catalina Channel, with sightings extending northwest from the Channel south of Pt. Dume.

Sighting occurrences for 1974-78 appeared to "clump" in the Catalina Channel area, extending from southeast of Long Beach to near Pt. Dume. 1978 sightings were more scattered throughout the area, except for high density areas of sightings southeast of Pt. Dume.

Index Trends.—The northern anchovy night index trend (Figs. 12, 13) was somewhat constant during 1963-69, with an average night index level of 3.50. The commercial catch increased sharply in 1969 and 1970, then declined in 1972. A period of warm sea surface temperatures which were well above average, occurred from August to December 1972 in the northeastern Pacific (Miller and Laurs 1975), and anomalous warm temperatures may have affected anchovy availability.

The index rose to 14.99 in 1973, and the commercial catch increased to near 117.9×10^3 t. Then, in 1974, a decline in index level and catch was evident. In 1975 the index increased to 11.38 and the catch increased to a record peak of 146.9×10^3 t. The catch decreased slightly in 1976 and 1977, then dropped to a very low level of about 16.3×10^3 t in 1978.

The aerial apparent abundance index declined in 1973-78 (see inspection fitted average line, Fig. 12), and this downward trend preceded the decline of the fishery. In 1975, the peak year of catch, the apparent abundance was not as great as it had been in 1973. However, sufficient fish were available in 1975, at an index level of 11.38, to meet the needs of the fishery. The 1978 apparent abundance index level of 1.91 was slightly below the index levels observed during the 1963-69 period. The total catch of anchovy in the central stock area, of which the southern California fishery is a part, was greater than the catch totals given in Figure 12, due to substantial quantities of anchovy landed and processed at Ensenada, Baja California, Mexico.

Night indices observed for the major fishing areas from near Santa Barbara to Dana Point, including the Channel Islands and San Pedro Channel, are shown in Figure 13. Zones G and H, the Catalina Channel, and the Catalina/14 mile bank area, were the major producing areas, and the highest indices were recorded for these areas. In 1978, a season of much reduced catches, the apparent abundance index increased for the Santa Barbara coastal area (zone C), the only anomalous trend observed.

Pacific Sardine

Morro Bay to San Nicolas Island.—1962-65, Fig. 14; 1966-69, Fig. 15.

The Pacific sardine fishery in the Monterey Bay area failed in the late 1940's. By the time the aerial monitoring survey program was started, little observation effort was being expended along the central California coast north of Morro Bay. In 1962-65, some flights were made along the coast from the south, to, and into, Monterey Bay. A few sardine schools were sighted in Monterey Bay but most were sighted along the coast south of Pt. Sur to Cape San Martin. Some schools were sighted from Morro Bay north (Fig. 14).

The last major catch of sardines off southern California was made near San Nicolas Island (lower right corner, Fig. 14), on opening day of the season, 1 September 1964. Prior to the season opening, aerial spotters estimated a maximum of about 9.1×10^3 t of sardines in the area. After the start of fishing, the sardine school group, which had been observed in the fishing area for 2 wk or more before the season opening, appeared to immediately start migrating southeast. After 2 d of fishing and a catch of about 2.7×10^3 t, only a few additional tons were taken in the San Nicolas Island area. During 1966-69 (Fig. 15), only a few small schools were sighted along the coast off Morro Bay, Avila, and Santa Barbara.

Pt. Hueneme to San Diego.—1962-65, Fig. 16; 1966-69, Fig. 17; 1970-73, Fig. 18.

During 1962-65, sardines were most frequently sighted in the San Pedro Channel south of Los Angeles Harbor, and near Catalina Island. In 1966-69, only six sightings were recorded off the Los Angeles area and southwest of San Clemente Island. The 1970-73 chart shows a small number of sightings off La Jolla, near San Diego. Since 1974, the aerial spotters have not sighted any individual schools of sardines.

Index Trends.—The pelagic resource aerial monitoring program was started after the major decline in sardine abundance occurred. However, the aerial index gives an insight into the last declining years of a once major resource (Fig. 19). In 1964, the catch was only about 6.4×10^3 t and the night index value was about 1.00; it was the last year sardines were caught in any quantity off southern California. In 1965, the index level declined to a very low level and has remained at a 0.00 level since. No individual schools of sardines have been recorded since 1973.

Pacific Bonito

Morro Bay to San Nicolas Island.—1962-65, Fig. 20; 1966-69, Fig. 21; 1970-73, Fig. 22; 1974-78, Fig. 23.

The geographical distribution of Pacific bonito sightings in this area changed little during the survey period. They were frequently sighted along the coast from east of Pt. Conception to near Ventura, around Anacapa Island, Santa Cruz Island, and near the southeast side of Santa Rosa Island. They were more frequently observed along the south side of Santa Cruz Island. During 1974-78, the frequency of sightings decreased, but the general distribution of sightings remained the same.

Pt. Hueneme to San Diego.—1962-65, Fig. 24; 1966-69, Fig. 25; 1970-73, Fig. 26; 1974-78, Fig. 27.

The geographical distribution of sightings changed little in this area from 1962 to 1978. As in the case of the northern anchovy, the distribution pattern of Pacific bonito since the mid-1960's has become more restricted, with sightings being found closer to the mainland coast and islands. The frequency of sightings peaked during 1966-69, with the major sighting area being from the Coronado Islands, Mexico, to Dana Point. In 1970-73, however, they were more commonly observed off San Diego. Sightings of Pacific bonito were fewer in number during 1974-78, and the 1978 sightings were primarily off Dana Point, Newport Beach, and Pt. Dume.

Index Trends.—Pacific bonito increased in abundance off California during the warm years of 1957-58 and was fished lightly between that time and 1965. Due to decreases in the availability or abundance of the Pacific sardine, Pacific mackerel, and jack mackerel, Pacific bonito became a target species. Catches off California more than doubled between 1965 and 1966, peaking with a catch of about 9.2×10^3 t.

The day apparent abundance index (Fig. 28) remained at an average level of 1.44, 1963-67, then decreased sharply to 0.43 in 1968, and to 0.26 in 1969. The catch declined about one-third during this period. No data was available for June-December 1970, but the first half-year data (normally low) indicated few schools were observed. The index increased to a peak of 1.11 in 1972, possibly due to an anomalous warm period in the northeastern Pacific during the summer and fall of 1972, which may have caused an increased migration of Pacific bonito into southern California from off northwestern Mexico. The index declined sharply in 1973 to 0.39, while catches off California increased to a level of about 8.2×10^3 t. The day index continued to decline over the years 1973-78 to a very low level, 0.12. Catches declined sharply in 1975 to the 1.8 to 2.7×10^3 t level and remained low, with a California catch of 1.2×10^3 t reported in 1978.

The major sighting areas for Pacific bonito (Fig. 29) were the Santa Barbara coast and Channel Islands (zones C and D) and the coastal area from near San Diego to Dana Point (zone J). The south coastal zone (J) had high index levels in 1963 and 1966 (record high for any one area) through 1971. The Santa Barbara coast and Channel zone (C) was the high index area for 1964, 1965, 1972, 1974, and 1975. Since 1972, index values for all areas declined to the low levels observed in 1977. In 1978, the night index increased to 0.94 as Pacific bonito were observed in greater quantities at night than during the day, a situation that occurred only in one other year, 1973.

Pacific Mackerel

Morro Bay to San Nicolas Island.—1962-65, Fig. 30; 1966-69, Fig. 31; 1974-78, Fig. 32.

In the area of Morro Bay to San Nicolas Island, Pacific mackerel were commonly sighted in the Santa Barbara Channel area and about the Channel Islands during 1962-65. Concentrations were sighted along the coast from east of Pt. Conception to near Ventura, with a center of sighting near Santa Barbara. Some schools were sighted along the north coast of Santa Cruz Island and the south side of Anacapa, and on the north side of San Nicolas Island. During 1966-69, only 21 schools or school groups were sighted, most of which were along the Santa Barbara coast. No schools were recorded for 1970 and 1974, but in 1977 and 1978, Pacific mackerel schools were again sighted about the Santa Barbara Channel Islands in large numbers, as shown on the 1974-78 charts. Between 1974 and 1977, 54 schools or school groups were recorded; in 1978, 74 were sighted.

During the 1962-65 period which preceded the decline of the Pacific mackerel resource to a very low level, most schools were sighted most frequently along the Santa Barbara coastline, and less frequently around Santa Cruz and Anacapa Islands. In contrast, during 1977 and 1978, only 11 schools or school groups were sighted along or near the Santa Barbara coast, while 117 schools or school groups were sighted off the north and southeast coasts of Santa Cruz Island and about Anacapa Island, indicating a shift in distribution pattern from the coast to about the Santa Barbara Channel Islands.

Pt. Hueneme to San Diego.—1962-65, Fig. 33; 1966-69, Fig. 34; 1970-73, Fig. 35; 1974-78, Fig. 36.

During 1962-65, the principal centers of sighting were around the east end of Catalina Island, and south of Long Beach. Pacific mackerel were also sighted at scattered locations along the coast from San Diego to Pt. Hueneme, and around San Clemente Island, Santa Barbara Island, and Cortez Bank. Few schools or school groups were sighted during 1966-69 or 1970-74, but a substantial

Table 3.—Annual indices of abundance for day and night observations. A dash (-/-) indicates no flight observations in the zone, 0.00 indicates observation effort in four places.

Zone	1962	1963	1964	1965	1966	1967	1968	1969	1970 (Jan. thru June)
NORTHERN ANCHOVY									
A	0.51/1.22	10.98/13.28	0.80/7.32	2.51/2.48	2.02/ 6.33	1.15/-	0.2820/-	0.00 /0.00	-/-
B	3.25/3.18	6.17/13.02	4.08/3.08	1.85/5.75	0.29/15.31	0.28/ 0.30	0.7346/-	0.0317/0.00	0.0714/-
C	0.05/0.99	0.40/ 2.70	0.90/2.85	1.82/8.63	0.27/ 2.79	2.91/ 3.03	0.0476/1.7637	0.8769/1.9387	0.3240/ 0.6387
D	0.00/2.97	1.24/10.02	0.23/4.75	0.48/3.67	0.14/ 6.73	0.63/ 5.12	0.0453/3.2438	0.4124/1.9662	0.0300/ 0.8163
E	-/0.00	0.00/ 1.05	0.00/3.14	0.00/0.12	1.09/ 0.23	3.15/ 0.11	0.1881/0.1284	0.3218/0.6701	0.6666/ 0.00
F	-/0.00	3.66/ 1.71	5.75/0.37	0.00/0.58	0.00/ 2.61	0.00/ 0.00	0.00 /0.6000	0.00 /0.00	-/ 0.00
G	-/1.00	0.51/ 1.81	0.54/6.21	1.42/3.23	2.24/ 1.78	2.40/ 8.32	0.5518/2.1056	5.0145/3.5780	31.7112/17.5166
H	-/-	0.14/ 0.12	0.38/1.00	0.05/1.90	2.28/ 1.43	5.45/ 1.60	0.6469/0.5820	6.3597/3.2604	17.9724/ 0.9949
I	-/-	0.14/ 0.00	0.05/0.11	0.02/0.34	0.28/ 2.53	2.87/ 0.71	0.1801/0.2116	0.7862/0.4971	0.00 / 0.8288
J	-/-	0.78/ 0.67	0.85/6.08	0.00/8.00	0.45/ 1.55	0.16/20.16	0.5282/1.1156	0.5536/3.3989	1.6282/46.5483
K	-/-	0.00/-	0.00/-	0.00/-	0.00/ 0.22	0.00/ 0.70	2.4400/0.0625	0.00 /0.00	-/-
L									
M									
N									
O									
P									
Average all zones	1.79/1.99	1.64/2.99	1.03/3.90	0.96/4.18	0.84/3.62	1.78/4.30	1.3274/1.4599	1.3043/4.3562	6.6325/8.8341
Average D+N						2.54	0.7183	2.4393	
PACIFIC BONITO									
A	0.00/0.00	0.00/0.00	0.50/0.00	0.00/0.00	0.04/0.00	0.07/-	0.0099/-	0.00 /0.00	-/-
B	0.01/0.00	0.00/0.01	0.06/0.01	0.02/0.00	0.43/0.00	0.01/0.00	0.00 /-	0.00 /0.00	0.00 /-
C	0.62/0.25	3.63/1.51	2.40/0.82	2.18/0.40	1.38/0.83	0.51/1.02	0.3617/1.3603	0.2994/0.2715	0.00 /0.0806
D	0.83/0.63	0.65/1.88	1.40/0.12	0.85/0.10	1.27/0.54	0.38/0.80	0.5285/0.1549	0.2433/0.2300	0.0057/0.5867
E	-/0.00	0.02/1.15	0.50/0.00	6.81/0.00	4.30/0.00	0.00/0.00	0.00 /0.0229	0.00 /0.00	0.00 /0.00
F	-/0.00	0.00/0.00	0.43/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00 /0.00	0.00 /0.00	-/0.00
G	-/0.00	0.31/0.37	0.30/0.00	0.50/0.01	1.19/0.16	0.67/0.39	0.1196/0.1302	0.1258/0.1666	0.0048/0.00
H	-/-	0.85/0.22	2.12/0.53	2 06/0.32	0.03/0.00	0.00/0.02	0.6805/0.2398	0.0907/0.0607	0.0689/0.0761
I	-/-	0.00/0.45	3.46/0.54	0.40/0.13	0.06/0.02	0.12/0.00	0.0275/0.0330	0.0203/0.0574	0.00 /0.1801
J	-/-	3.67/0.23	1.10/0.06	1.71/0.46	4.96/0.11	3.27/0.12	1.7038/0.6872	0.6464/0.0518	0.00 /0.00
K	-/-	0.13/-	0.00/-	0.00/-	0.00/0.00	45.73/0.00	0.2666/0.00	0.7547/0.00	-/-
L									
M									
N									
O									
P									
Average all zones	0.23/0.19	1.62/0.68	1.62/0.28	1.26/0.19	1.34/0.35	1.35/0.34	0.4325/0.3477	0.2682/0.1815	0.0059/0.1000
Average D+N						1.05	0.4032	0.2359	
JACK MACKEREL									
A	0.00/0.08	1.81/ 0.00	8.32/2.89	0.78/ 1.67	4.29/25.72	0.81/-	0.9153/-	0.0290/ 0.00	-/-
B	0.02/0.00	3.48/ 1.37	6.65/6.67	1.03/ 1.22	0.74/ 8.78	0.78/ 1.34	0.6966/-	0.00 / 0.00	0.00 /-
C	1.59/0.45	0.96/ 0.49	0.83/0.56	0.14/ 0.33	0.06/ 0.03	0.04/ 0.33	0.1319/ 0.0238	0.1150/ 0.1725	0.3065/ 0.3225
D	0.00/1.45	1.79/13.77	2.72/5.36	1.44/ 1.40	0.24/ 1.62	0.41/ 0.24	0.2064/ 0.1962	0.1544/ 0.3300	0.0607/ 0.1785
E	-/0.00	0.27/ 4.74	0.93/2.31	0.72/ 1.55	0.16/ 7.38	0.00/ 2.15	0.2475/ 4.0917	0.00 / 4.4175	0.00 / 0.00
F	-/2.91	11.16/39.70	1.63/2.31	0.00/17.41	0.00/27.91	0.00/38.84	10.8714/27.7731	3.5696/13.0833	-/12.3148
G	-/-	1.23/ 1.76	0.64/0.99	0.02/ 0.29	0.00/ 1.05	0.00/ 0.10	0.0239/ 0.0072	0.1394/ 0.2673	0.0339/ 0.0119
H	-/-	0.56/ 1.34	0.01/1.11	0.71/ 0.43	0.04/ 2.18	0.01/ 0.33	0.00 / 0.2665	0.00 / 0.5998	0.0172/ 0.3045
I	-/-	2.11/ 5.53	0.17/1.86	1.35/ 0.75	0.19/ 2.37	0.04/ 3.27	0.0045/ 1.2764	0.0489/ 1.5833	0.4090/ 0.7432
J	-/-	0.67/ 0.54	0.72/1.51	0.86/ 0.96	0.00/ 0.06	0.00/ 0.03	0.0855/ 1.0799	0.0616/ 0.3058	0.6410/ 2.1129
K	-/-	0.00/-	0.00/-	0 00/-	0.00/ 0.00	0.00/ 1.75	0.00 / 1.0937	0.00 . / 0.00	-/-
L									
M									
N									
O									
P									
Average all zones	0.51/0.46	1.41/2.98	1.62/2.18	0.71/1.36	0.28/1.94	0.20/1.41	0.3044/2.2488	0.1119/0.6562	0.1648/0.5843
Average D+N						0.56	0.9754	0.3143	

zone but no fish sighted. Indices given as day/night. 1962 to 1967 data inconsistent regarding number of decimal places, all to two places plus; after 1968 all carried to

1971	1972	1973	1974	1975	1976	1977	1978
-/-	-/-	0.2857/-	0.00 /-	-/-	-/-	-/-	-/-
0.2592/0.00	0.00 /0.00	1.1111/ 7.6222	0.00 /-	0.1250/ 0.00	0.00 / 0.3030	0.304 /0.00	0.00 /-
0.6580/3.0459	0.8916/1.9063	0.5449/ 8.0520	0.2983/ 7.1637	4.1790/ 5.3511	3.6930/ 4.0366	4.23 /2.913	0.3478/8.3585
0.1368/2.1839	0.3668/0.7927	1.8384/ 1.7935	1.4139/ 5.2212	1.6621/ 4.0351	1.2133/ 4.1187	4.678 /6.34	7.5962/1.9864
0.2295/0.00	0.00 /0.1346	0.1200/ 0.00	0.7010/ 0.00	0.00 / 0.00	0.00 / 0.00	0.00 /0.054	0.8298/0.00
0.00 /0.00	0.00 /0.0674	16.2553/ 0.00	6.3235/ 1.3113	0.00 / 0.00	0.00 / 0.00	0.00 /0.00	0.00 /0.00
6.5099/8.7620	5.7211/3.5333	8.0516/25.7464	7.5068/11.3228	10.9772/18.1811	3.3894/ 8.4065	3.794 /6.6817	1.3494/1.1229
3.1002/1.1379	0.7711/0.0522	6.5606/18.8580	4.7102/ 6.8398	1.4856/ 2.0287	2.2903/ 3.0512	1.408 /2.059	1.3961/0.1747
0.3917/0.1228	0.5371/0.1363	2.1185/ 7.2598	0.3564/ 2.6627	0.2514/ 0.00	0.00 / 0.8730	0.4216/0.1498	1.6298/0.5993
0.7907/0.0555	1.5934/0.00	0.4207/ 9.2647	1.3235/ 0.1707	0.9050/ 1.3255	0.4436/10.0188	1.3015/2.253	2.3155/0.0354
0.00 /-	0.00 /0.00	0.2732/ 0.00	0.1403/ 4.0588	0.00 /-	0.00 / 0.0952	0.028 /-	0.8249/-
		0.1996/ 0.00	0.00 /-	1.3075/-	0.0080/ 0.0615	0.1430/2.307	3.1106/-
		0.00 / 0.00	0.00 /-	0.00 /-	0.00 /-	0.00 /-	0.00 -
		0.00 /-	0.3216/-	0.00 /-	0.3265/ 0.00	0.9308/0.6909	0.00 -
		-/-	0.00 /-	-/-	-/-	-/-	-/-
		0.1273/-	0.00 /-	0.00 /-	0.0293/ 0.00	2.765/0.2413	0.00 /-
1.1893/2.3107	1.3155/1.4058	2.4401/14.9912	2.0443/7.9060	3.9212/11.3889	1.5046/5.3696	2.1849/4.639	2.0742/1.9153
1.5962	1.3486	5.8869	3.8738	6.0923	2.2800	3.4003	2.0118
-/-	-/-	0.00 /-	0.00 /-	-/-	-/-	-/-	- -
0.00 /0.00	1.7808/0.00	0.5158/0.00	3.5294/-	0.00 /0.00	0.00 /0.00	0.00 /0.00	-/-
0.1971/0.8846	2.0008/0.6135	1.0244/0.9090	0.8467/1.0172	0.4319/0.00	0.2324/0.0076	0.1741/0.00	0.1085/0.00
0.1732/0.0324	0.4746/0.1506	1.3562/0.8664	0.0776/0.0075	0.4005/0.0067	0.1595/0.00	0.00 /0.00	0.00 /1.9514
0.0409/0.00	0.00 /0.061	0.00 /0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00
0.00 /0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00	0.008 /0.0253	0.00 /0.00
0.1627/0.0094	0.0036/0.0031	0.1318/0.0707	0.0043/0.0098	0.0014/0.0035	0.0118/0.00	0.0109/0.00	0.1039/0.6735
0.00 /0.0029	0.00 /0.0672	0.0220/0.0453	0.0051/0 0188	0.00 /0.00	0.0067/0.00	0.0109/0.00	0.00 /0.0075
0.0128/0.00	0.00 /0.0239	0.0098/0.0196	0.0166/0.00	0.00 /0.00	0.0129/0.00	0.00 /0.5381	0.00 /0.0177
2.6452/0.8333	0.0102/0.00	0.8039/0.0490	0.3975/0.00	0.0035/0.00	0.1817/0.00	0.1020/0.053	0.8451/6.2247
0.2857/-	0.00 /0.00	0.00 /0.00	0.0054/0.00	0.00 /-	0.00 /0.00	0.00 /-	0.00 /-
		0.1068/0.00	0.0710/0.00	0.00 /-	0.0013/0.00	0.00 /0.00	0.00 /-
		0.00 /0.00	0.00 /-	0.00 /-	0.00 /-	0.00 /-	0.00 /-
		0.0056/-	0.1444/0.00	0.00 /-	0.00 /0.00	0.00 /0.00	0.00 /-
		-/-	0.00 /-	-/-	-/-	-/-	- -
		0.00 /-	0.00 /-	0.8928/-	0.00 /0.00	0.00 /0.00	0.00 /-
0.5530/0.1516	1.1171/0.1993	0.3944/0.3902	0.2492/01775	0.0860/0.0027	0.0748/0.0021	0.0390/0.0386	0.1268/0.9380
0.4073	0.7807	0.3932	0.2268	0.0608	0.0602	0.0388	0.4455
-/-	-/-	0.00 /-	0.00 /-	-/-	-/-	-/-	- -
0.00 / 0.00	0.00 /0.00	0.00 /0.00	0.00 /-	0.00 / 0.00	0.00 /0.00	0.00 / 0.00	-/-
0.0267/ 0.0600	0.0024/0.0050	0.0018/0.00	0.00 /0.0948	0.00 / 0.0413	0.00 /1.4669	0.0223/ 0.5589	0.0089/ 0.00
0.0632/ 0.0216	0.0071/0.2349	0.00 /0.00	0.0032/0.0151	0.00 / 0.0067	0.3110/1.2332	0.2959/ 3.1454	0.1687/ 1.8643
0.00 / 5.4017	0.00 /0.0961	0.00 /0.00	0.00 /6.1830	0.00 / 0.6250	0.00 /0.00	0.00 / 1.3949	0.00 / 0.9315
3.3700/10.4297	0.00 /6.4061	0.3723/0.6862	1.3088/3.3473	0.00 /37.5000	0.7614/4.0483	0.00 /27.2615	9.1818/14.6290
0.0180/ 0.1581	0.0036/0.0534	0.0156/0.0415	0.0172/0.0984	0.00 / 0.0172	0.0768/0.1725	0.3359/ 1.5846	2.4415/ 4.9477
0.00 / 1.3275	0.00 /0.3417	0.00 /0.0075	0.0357/0.1190	0.2396/ 2.0881	0.0271/1.5528	0.2008/ 3.6547	2.3239/10.8547
0.0128/ 1.1978	3.5087/0.3480	0.00 /1.0669	0.0367/0.9224	0.6814/ 5.7410	0.1077/1.6349	0.7458/ 0.7779	5.2704/ 1.8989
0.0148/ 0.00	0.0205/0.00	0.0012/0.00	0.0051/0.00	0.00 / 0.00	0.1362/0.00	0.1275/ 0.2298	0.00 / 0.00
0.00 /-	0.0641/0.00	0.0206/0.00	0.00 /0.00	0.00 /-	0.00 /0.00	0.0354/-	0.00 /-
		0.00 /0.00	0.00 /-	0.00 /-	0.00 /0.00	0.00 / 0.00	0.00 /-
		0.00 /0.00	0.00 /-	0.00 /-	0.00 /-	0.00 /-	0.00 /-
		0.00 /-	0.00 /-	0.00 /-	0.00 /0.00	0.00 / 0.00	0.00 /-
		-/-	0.00 /-	-/-	-/-	-/-	0.00
		0.00 /-	0.00 /-	0.00 /-	0.00 /0.00	0.00 / 0.00	0.00
0.0449/0.9225	0.1325/0.7388	0.0066/0.0603	0.0274/0.4350	0.0761/0.4013	0.0817/0.8735	0.1944/2.7751	1.1847/4.2077
0.3633	0.6983	0.0213	0.1546	0.1708	0.2406	1.4726	2.3724

Table 3.—*Continued.*

Zone	1962	1963	1964	1965	1966	1967	1968	1969	1970 (Jan. thru June)
PACIFIC MACKEREL									
A	0.00/ 0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/-	0.00/-	0.00/0.00	-/-
B	0.30/ 0.03	0.00/1.56	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/-	0.00/0.00	0.00/0.00
C	0.00/ 3.15	0.23/0.37	0.03/0.30	0.04/0.28	0.01/0.35	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
D	0.50/ 0.30	1.41/2.20	0.49/0.23	0.05/0.08	0.00/0.01	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
E	-/ 3.75	0.43/0.67	0.02/0.74	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.0366	0.00/0.00	0.00/0.00
F	-/ 0.00	5.40/6.59	3.15/3.62	0.00/0.23	0.00/2.95	0.00/0.00	0.00/0.0051	0.00/0.00	0.00/0.00
G	-/18.75	0.79/0.46	0.78/0.13	0.00/0.44	0.00/0.04	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
H	-/-	2.19/1.62	0.14/0.36	0.00/0.02	0.00/0.02	0.00/0.00	0.00/0.0042	0.00/0.0347	0.00/0.0050
I	-/-	0.76/0.40	0.01/0.53	0.00/0.11	0.00/0.09	0.00/0.02	0.00/0.00	0.00/0.0402	0.00/0.0180
J	-/-	0.83/1.44	0.75/0.29	0.00/0.36	0.00/0.06	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
K	-/-	1.94/-	0.00/-	0.00/-	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	-/-
L									
M									
N									
O									
P									
Average all zones	0.17/1.26	0.79/0.91	0.33/0.33	0.01/0.19	0.00/0.14	0.00/0.00	0.00/0.0022	0.0001/0.0096	0.00/0.0028
Average D + N						0.0020	0.0007	0.0036	
PACIFIC SARDINE									
A	0.00/ 0.00	1.40/3.78	1.22/0.05	0.04/0.00	0.00/0.00	0.00/-	0.00/-	0.00/0.00	-/-
B	0.05/ 2.13	0.31/0.00	0.26/1.63	0.00/0.00	0.00/0.38	0.00/0.00	0.00/0.00	0.00/0.00	0.00 /-
C	0.04/ 0.00	0.02/0.00	0.00/0.05	0.07/0.02	0.00/0.00	0.00/0.03	0.00/0.00	0.00/0.00	0.00 /0.00
D	0.00/ 0.28	0.07/2.36	0.23/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00 /0.00
E	-/12.50	2.22/0.83	1.75/7.87	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00 /0.00
F	-/ 0.00	0.00/0.00	13.47/1.62	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	-/0.00	0.00 /0.00
G	-/ 0.00	0.08/0.30	0.17/0.13	0.03/0.00	0.00/0.09	0.00/0.00	0.00/0.00	0.00/0.00	0.00 /0.00
H	-/-	0.06/0.67	0.00/2.27	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.0213	0.00/0.00	0.00 /0.00
I	-/-	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.02	0.00/0.00	0.00/0.00	0.00/0.00	0.00 /0.00
J	-/-	0.12/0.05	0.22/0.01	0.00/1.09	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.2564/0.00
K	-/-	0.00/-	0.00/-	0.00/-	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	-/-
L									
M									
N									
O									
P									
Average all zones	0.04/1.00	0.22/0.50	0.27/1.03	0.02/0.05	0.00/0.04	0.00/0.0078	0.00/0.0022	0.00/0.00	0.0067/0.00
Average D + N						0.0023	0.0007	0.0000	
PACIFIC BARRACUDA									
A	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/-	0.00 /-	0.00 /0.00	-/-
B	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.24/0.00	0.00/0.00	0.00 /-	0.00 /0.00	0.00
C	0.00/0.00	0.34/0.43	0.45/0.48	0.25/0.00	0.02/0.00	0.02/0.00	0.0382/0.0119	0.0422/0.00	0.0199/0.00
D	0.00/0.00	0.00/0.00	0.00/0.01	0.00/0.00	0.01/0.00	0.00/0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00
E	-/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00
F	-/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00 /0.00	0.00 /0.00	-/0.00
G	-/0.00	0.00/0.11	0.00/0.00	0.02/0.00	0.00/0.00	0.00/0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00
H	-/-	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.11/0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00
I	-/-	0.15/0.00	0.00/0.31	0.40/0.00	0.02/0.00	0.01/0.00	0.00 /0.00	0.0016/0.00	0.00 /0.00
J	-/-	0.04/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00 /0.00	0.0429/0.00	0.00 /0.00
K	-/-	0.00/-	0.00/-	0.00/-	0.00/0.00	0.00/0.00	0.00 /0.00	0.00 /0.00	-/-
L									
M									
N									
O									
P									
Average all zones	0.00/0.00	0.08/0.15	0.08/0.12	0.10/0.00	0.03/0.00	0.00/0.00	0.0077/0.0016	0.0183/0.00	0.0084/0.00
Average D + N						0.0035	0.0056	0.0115	

1971	1972	1973	1974	1975	1976	1977	1978
-/-	-/-	0.00/-	0.00/-	-/-	-/-	-/-	
0.00/-	0.00/0.00	0.00/0.00	0.00/-	0.00/0.00	0.00/0.00	0.00/0.00	0.00
0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.006/0.021	0.0092/0.0658
0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.0394	0.357/1.31	1.1879/5.0309
0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.1292/0.00	0.00/0.00	3.4574/23.8452
0.6744/0.00	0.00/0.2932	0.00/2.2058	0.00/0.00	0.00/0.00	0.00/0.00	0.223/8.0	2.7273/18.1452
0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.006/0.82	1.1853/4.4186
0.0990/0.1315	0.00/0.0047	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	5.45/8.41	9.6584/13.3682
0.0025/0.0451	0.00/0.0492	0.00/0.00	0.00/0.00	0.0446/0.00	0.4707/0.00	3.61/13.89	8.4372/30.2404
0.0005/0.00	0.0041/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.0068/0.00	0.009/0.062	0.6338/4.9126
0.00/-	0.00/0.00	0.00/0.00	0.00/0.00	0.00/-	0.00/0.00	0.00/-	0.00
		0.00/0.00	0.00/-	0.00/-	0.00/0.00	0.00/0.00	0.00/-
		0.00/0.00	0.00/-	0.00/-	0.00/-	0.00/-	0.00
		0.00/-	0.00/-	0.00/-	0.00/0.00	0.00/0.00	0.00
		-/-	0.00/-	-/-	-/-	-/-	
		0.00/-	0.00/-	0.00/-	0.00/0.00	0.00/0.00	0.00/-
0.0042/0.0028	0.0003/0.0338	0.0000/0.0282	0.00/0.00	0.0035/0.00	0.0285/0.0066	0.907/2.62	2.1831/7.4608
0.0233	0.0126	0.0077	0.00	0.0025	0.0241	1.754	4.2566
-/-	-/-	0.00/-	0.00/-	-/-	-/-	-/-	-/-
0.00/0.00	0.00/0.00	0.00/0.00	0.00/-	0.00/0.00	0.00/0.00	0.00/0.00	0.00/-
0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
0.00/0.1000	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
0.0207/0.00	0.0205/0.00	0.0102/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
0.00/-	0.00/0.00	0.00/0.00	0.00/0.00	0.00/-	0.00/0.00	0.00/-	0.00/-
		0.00/0.00	0.00/-	0.00/-	0.00/0.00	0.00/0.00	0.00/-
		0.00/0.00	0.00/-	0.00/-	0.00/-	0.00/-	0.00/-
		0.00/-	0.00/-	0.00/-	0.00/0.00	0.00/0.00	0.00/-
		-/-	0.00/-	-/-	-/-	-/-	-/-
		0.00/-	0.00/-	0.00/-	0.00 00.0	0.00/0.00	0.00/-
0.0030/0.0008	0.0015/0.00	0.019/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
0.0023	0.0010	0.0013	0.00	0.00	0.00	0.00	0.00
-/-	-/-	0.00/-	0.00/-	-/-	-/-	-/-	-/-
0.00/0.00	0.00/0.00	0.00/0.00	0.00/-	0.00/-	0.00/0.00	0.00/0.00	0.00/-
0.0125/0.00	0.00/0.00	0.0037/0.00	0.2688/0.00	0.0252/0.00	0.0396/0.00	0.00/0.00	0.00/0.00
0.00/0.00	0.0856/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
0.00/0.00	0.00/0.00	0.00/-	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
0.00/0.00	0.00/0.00	-/-	0.0068/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
0.00/-	0.00/0.00	0.00/-	0.00/0.00	0.00/-	0.00/0.00	0.00/-	0.00/-
		0.00/0.00	0.00/-	0.00/-	0.00/0.00	0.00/0.00	0.00/-
		0.00/0.00	0.00/-	0.00/-	0.00/-	0.00/-	0.00/-
		0.00/-	0.00/-	0.00/-	0.00/0.00	0.00/0.00	0.00
		-/-	0.00/-	-/-	-/-	-/-	
		0.00/-	0.00/-	0.00/-	0.00/0.00	0.00/0.00	0.00/-
0.0055/0.00	0.0190/0.00	0.0004/0.00	0.0407/0.00	0.0030/0.00	0.0053/0.00	0.00/0.00	0.00/0.00
0.0035	0.0120	0.0003	0.0260	0.0021	0.0042	0.00	0.00

Table 3.—*Continued.*

Zone	1962	1963	1964	1965	1966	1967	1968	1969	1970 (Jan. thru June)
YELLOWTAIL									
A	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/-	0.00 /-	0.00/0.00	-/-
B	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.07/0.00	0.00/0.00	0.00 /-	0.00/0.00	0.00/-
C	0.00/0.00	0.03/0.04	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00 /0.00	0.00/0.00	0.00/0.00
D	0.00/0.00	0.36/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00 /0.00	0.00/0.00	0.00/0.00
E	-/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00 /0.00	0.00/0.00	0.00/0.00
F	-/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00 /0.00	0.00/0.00	-/0.00
G	-/0.00	0.00/0.00	0.00/0.00	0.01/0.00	0.00/0.00	0.00/0.00	0.00 /0.00	0.00/0.00	0.00/0.00
H	-/-	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00 /0.00	0.00/0.00	0.00/0.00
I	-/-	0.55/0.64	0.13/0.04	0.34/0.07	0.39/0.00	0.09/0.00	0.00 /0.00	0.00/0.00	0.00/0.00
J	-/-	0.63/0.10	0.00/0.00	0.16/0.00	0.00/0.00	0.00/0.00	0.0037/0.00	0.00/0.00	0.00/0.00
K	-/-	0.00/-	0.00/-	0.00/-	0.00/0.00	0.00/0.00	0.00 /0.00	0.00/0.00	-/-
L									
M									
N									
O									
P									
Average all zones	0.00/ 0.00	0.19/ 0.06	0.01/ 0.00	0.06/ 0.00	0.04/ 0.00	0.00/ 0.00	0.0004/ 0.00	0.00/0.00	0.00/0.00
Average D - N						0.0023	0.0002	0.0000	—

increase in sightings occurred in this area during 1976-78. In 1976, 11 sightings were made about San Clemente Island, and 3 northwest of San Diego. In 1977, sightings totaled 210 with concentrations about Catalina and San Clemente Islands, and a small group of sightings about Cortez Bank and along the coast near Pt. Dume. Most of the increase in numbers of sightings occurred in the late summer and fall of 1977. In 1978, 321 sightings were made, and were concentrated about the southern California islands, including Santa Barbara Island. An increasing number of sightings occurred in the Catalina Channel south of Long Beach, and along the coast both east and west of Pt. Dume.

In recent years, Pacific mackerel have been sighted in many of the same areas as during the 1962-65 period, the exception being that sightings are not as common in the San Diego to Oceanside area.

Index Trends.—The aerial pelagic resource monitoring program was started after the major decline of the Pacific mackerel fishery had occurred. However, about the time the survey program was started (1963), and in the years following, a sequence of severe recruitment failures helped reduce the population to a very low level (MacCall et al. 1976). The biomass estimate in 1962 was about 99.8×10^3 t. By 1963, it had declined to about 54.4×10^3 t, and to a level of about 7.3×10^3 t in 1967. A catch moratorium was placed on the commercial fishery in 1970. In later years, this was modified and catches off California in 1977 and 1978 amounted to 3.8 and 13.2×10^3 t, respectively. The night index (Fig. 37) declined from about 0.91 in 1963 to 0.00 in 1967 and remained at a very low level through an 8-yr period, from 1967 to 1975. The catch also declined sharply from 18.1×10^3 t in 1963 to about 2.3×10^3 t in 1965. Historical records would indicate the Pacific mackerel is subject to rather severe fluctuations in recruitment. In 1976, a small increase in the index level was evident, and in 1977 the index level had increased dramatically to a level of about 2.62. In 1978, the 1977 level increased 2.8 times, to a level of 7.46. Within a 3-yr period, the Pacific mackerel went from zero observations of pure schools in 1974, to a condition in 1978 where it was one of the species frequently observed in substantial tonnage.

Jack Mackerel

Morro Bay to San Nicolas Island.—1962-65, Fig. 38; 1966-69, Fig. 39; 1970-73, Fig. 40; 1974-78, Fig. 41.

Jack mackerel were frequently sighted along the coast from Avila northward to Pt. Sur, and from Pt. Conception eastward in the Santa Barbara Channel, with centers of sightings in the Channel southeast of Santa Barbara about the eastern half of Santa Cruz Island, and Anacapa Island. Observations on the flight log charts, from 1962 through 1969, showed little change in areas and numbers sighted. Fewer sightings were made during 1970-73 about the Santa Barbara coast, Channel, and Islands, and this may have been related to the oil discharge in the Santa Barbara Channel in early 1970. During this period, less search effort was expended north of Pt. Conception, but the effort that was expended failed to note any concentrations. During 1976-78, jack mackerel were sighted in increasing numbers at the eastern end of the Santa Barbara Channel, and about Santa Cruz and Anacapa Islands, in the same areas as observed during 1962-69.

Pt. Hueneme to San Diego.—1962-65, Fig. 42; 1966-69, Fig. 43; 1970-73, Fig. 44; 1974-78, Fig. 45.

For the area from Pt. Hueneme to San Diego, there has been little change in the major sighting areas since 1962. Sightings declined during 1970-73, as in the Santa Barbara Channel area. In 1976-78, the sightings increased along the coast and about the islands and on Cortez Bank. During this period, the coastal area from southwest of Pt. Dume to Pt. Hueneme appeared to have a greater number of sightings than during 1962-65.

Index Trends.—The aerial night index level (Fig. 46) was about 2.98 in 1963, with a catch of 42.6×10^3 t. In 1964-67, the catch declined about one-third, but the aerial index did not show a declining trend. In 1969, the index dropped sharply to a 0.65 level and continued to decline through 1975 (0.40). In 1976, a small increase in the index was noted (0.87), rising to 2.77 in 1977. It then increased 1.5 times in 1978 to a record high of 4.20. The substantial increase in index level in 1977 and 1978 parallels, but does not equal in magnitude, the increase in the Pacific mackerel index. Both day and night indices for jack mackerel increased in 1978.

1971	1972	1973	1974	1975	1976	1977	1978
-/-	-/-	0.00 /-	0.00 /-	-/-	-/-	-/-	-/-
0.00/0.00	0.00 /0.00	0.00 /0.00	0.00 /-	0.00 /0.00	0.00 /0.00	0.00/0.00	0.00/-
0.00/0.00	0.0664/0.00	0.0074/0.00	0.0044/0.00	0.00 /0.00	0.00 /0.00	0.00/0.00	0.00/0.00
0.00/0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00	0.0014/0.00	0.00/0.00	0.00/0.00
0.00/0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00	0.0873/0.6451	0.00/0.00	0.00/0.00
0.00/0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00	0.00/0.00	0.00/0.00
0.00/0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00	0.00/0.00	0.00/0.00
0.00/0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00	0.00/0.00	0.00/0.00
0.00/0.00	0.0109/0.00	0.00 /0.00	0.00 /0.00	0.0047/0.00	0.00 /0.00	0.00/0.00	0.00/0.00
0.00/-	0.00 /0.00	0.0460/0.00	0.2364/0.00	0.00 /0.00	0.00 /0.00	0.00/0.00	0.00/00.0
0.00/0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00	0.00 /-	0.00 /0.00	0.00/-	0.00/-
		0 00 /0.00	0.0106/-	0.00 /-	0.00 /0.00	0.00/0.00	0.00/-
		0.00 /0.00	0.00 /-	0.00 /-	0.00 /-	0.00/-	0.00/-
		0.2847/-	0.00 /-	0.00 /-	0.00 /0.00	0.00/0.00	0.00/-
		-/-	0.00 /-	-/-	-/-	-/-	0.00/-
		0.00 /-	0.00 /-	0.00 /-	0.00 /0.00	0.00/0.00	0.00/-
0.00/0.00	0.0035/0.00	0.0213/0.00	0.0470/0.00	0.0004/0.00	0.0015/0.0056	0.00/0.00	0.00/0.00
0.0000	0.0022	0.0155	0.0323	0.0003	0.0024	0.00	0.00

Bluefin tuna						
A	0.00 /-	0.00 /-	-/-	-/-	-/-	-/
B	0.00 /0.00	0.00 /-	0.00 /0.00	0.00 /0.00	0.00 /0.00	0.00 /0 00
C	0.00 /0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00
D	0.00 /0.00	0.0226/0.00	0.0386/0.00	0.00 /0.00	0.00 /0.00	0.00 /0.00
E	0.00 /0.00	0.0257/0.00	0.3281/0.00	0.0545/0.00	0.00 /0.00	0.00 /0.00
F	0.00 /0.00	0.6127/0.0449	0.00 /0.00	0.0458/0 7258	0.00 /0.00	0.00 /0.00
G	0.00 /0.00	0.0797/0 0410	0.0241/0.00	0.00 /0.0021	0.00 /0.00	0.00 /0.00
H	0.00 /0.00	0.0306/0.00	0.0279/0 00	0.0067/0 00	0.0072/0.00	0.00 /0.00
I	0.2667/0.00	0.2603/0.00	0.1228/0 00	1.2857/0 0396	0.034 /0.00	0.00 /0.00
J	0.0408/0.00	0.7556/0.00	0.0779/0.00	0.7330/0.00	0.00 /0.00	0.00 /0.00
K	3.0506/1.2878	1.9407/0.00	0.1034/-	1.6140/0 2380	0.14 /-	4.145/-
L	1.1499/0.5319	1.9779/-	0.3642/-	1.6190/0.00	0.00 /0.00	0.328/
M	2.9545/0.00	0.00/-	0.00 /-	0.00 /-	0.00 /-	0.00 /-
N	2.4402/-	5.3768/-	0.7735/-	1.7961/0.00	4.44 /0.00	9.482/-
O	-/-	0.00/-	-/-	-/-	-/-	-/
P	16.3561/	14.3181/-	0.00 /0.00	0.2495/0.00	0.037/0.00	2.142/
Q						
R				24.7204/0.00	-/-	-/-
Average all zones	0.9462/0.0276	0.7972/0.0202	0.1324/0.00	0.8766/0.0091	0.424/-	0.7183/0.00
Average D+N	0.6940	0.5547	0.0938	0.7026	0.2139	0.4361

Tunas

Bluefin tuna.—Sightings of bluefin tuna for all years 1962 through 1978, are given for the areas north of the United States-Mexico border (Figs. 47, 48), and for the area from San Diego south into Mexico (Fig. 49). Flight log charts for areas south of the border (see dotted line on Fig. 49) were not used by the program until 1974.

Figure 47 shows that the major sighting area for bluefin tuna in the Santa Barbara Channel and Channel Islands area was along the south side of Santa Cruz and Santa Rosa Islands, with a few sightings made near San Nicolas Island and along the Santa Barbara coast. Figure 48 shows that sightings were widely scattered west and southwest of San Diego. Bluefin tuna were frequently sighted about San Clemente Island, and along the coasts off Oceanside and Redondo Beach. In the southern area of fishing off Mexico (Fig. 49), sightings were more concentrated west and northwest of Ensenada. Aerial spotter operations were seldom conducted south of Pta. Baja, Mexico.

Index Trends.—For the period 1973-78 day index (Table 2), the index trend shows 1975 to have been the lowest in relative apparent abundance (0.13). The highest level was recorded in 1973 (0.95).

Albacore tuna.—For albacore tuna sightings, Figure 50 gives locations for all years 1962 through 1978. Figure 51, from the Coronado Islands, Mexico, southward to Pta. Baja, indicates sightings for the years 1974-78.

Albacore were sometimes sighted west and southwest of San Diego (Fig. 50), but few sightings were made north of this area. A total of 124 sightings were made during the survey period. Figure 51 indicates that 76 sightings were made west to northwest of Ensenada, but few were made in this area south of a line drawn west from Cabo Colnett, Mexico.

Other sightings

Although yellowtail, Pacific barracuda, white seabass, basking shark, and squid are not of primary interest to the commercial aerial fish spotter, records were maintained and are given for these species because they are of interest to the recreational or commercial fisheries of southern California.

Yellowtail.—Areas of sighting were about the Coronado Islands, Mexico, north to near Newport, along the northeast side of San Clemente Island (Fig. 52), and along the coast from Santa Barbara to Pt. Conception (Fig. 53)

Pacific barracuda.—Small numbers of sightings were made along the coast, from north of San Diego to near Long Beach, and off the northeast side of San Clemente Island (Fig. 54). Barracuda were also sighted along the coast from near Pt. Conception to Ventura (Fig. 55).

White seabass.—This species was more commonly sighted by the aerial spotters near Pt. Conception, along the north side of Santa Cruz Island (Fig. 56), and to the north off Avila, Morro Bay (Fig. 57), with some sightings recorded in the northern half of Monterey Bay.

Observations of basking shark (Figs. 58, 59) and of squid (Figs. 60, 61) are of interest to the commercial fishery and are given. Index values are not given for these species.

Basking shark.—Although many species of sharks were sighted, most were not indentified by the spotter pilots as to species. The exceptions were the large sharks, such as the basking shark which was the subject of a commercial fishery in the late 1940's and early 1950's. Aircraft were used in this fishery to locate basking sharks and, on occasions, great white sharks were observed (Squire 1967).

Basking sharks were quite common in coastal waters in the late 1940's and early 1950's, and at that time were fished commercially in California. They were sighted frequently off Avila and Morro Bay (Fig. 58) along the coast south of Pt. Sur, but most frequently in the central and northern half of Monterey Bay (Fig. 59). Few were observed in the mid- to late-1960's and early 1970's. Recently, more basking sharks were being sighted north along the coast from the Santa Barbara area west to Point Conception. A total of 1,911 basking sharks were recorded by the aerial spotters.

Squid.—The only invertebrate animal reported as being sighted in surface schools was the squid. Schools were most common about the eastern half of Santa Cruz Island and Anacapa Island (Fig. 60), and in the coastal area from Pt. Hueneme to Pt. Dume. They appeared most common about Catalina Island (Fig. 61), with larger concentrations along the southwest side. Distribution of sightings about San Clemente Island were grouped at the northwest and southeast ends.

DISCUSSION

Evaluation of Index Data

The aerial observation program relies on the assistance of commercial aerial spotters who, for a modest fee, provide flight log data. The limitations of the data must be recognized since they are nonrandom, and influenced by many variable factors.

Sighting.—The probabilty of sighting a school may be affected by a number of physical factors, some of which are common to both day and night operations, others to day or night (see Table 4). Economic factors are also very important in determining target species for search and location of area searched. In recent years, the demand for anchovy has increased and additional emphasis has been placed on searching areas where anchovy are commonly observed. However, these areas are frequently the same areas where other species are observed.

Table 4.—Physical factors affecting the probability of sighting a school. X = important, — = less important, and 0 = not a factor.

	Day	Night
Area observed	X	X
Angle of viewing	X	—
Sun position	X	0
Moon phase	0	X
School size	X	X
School depth	X	X
School density	X	—
Bioluminescence levels	0	X
Weather		
clear	X	0
overcast	X	0
haze	X	—
Configuration of aircraft	X	X
Ground speed differences	—	—

Identification.—The detection of near-surface schools during the day is dependent upon the pilot's ability to distinguish subtle color and light intensity differences in the water. Detection of schools at night is possible only during the dark phase of the moon, and depends on the pilot's ability to discern gradation of light intensity. Bioluminescence of planktonic organisms agitated by schooling fish indicates by a dull glow the location and size of the school.

Species are identified during the day on the basis of a combination of two or more of the following characteristics: color of school or individual fish, shape of school, and behavior and size of individuals within the school. At night, species identification is based on shape of the luminous area and behavior of the schooling fish under undisturbed conditions, or by the behavior of the school after being subjected to a stimulus from an external source such as a flash from the aircraft's landing light. A light flash causes a response or movement of the fish, which agitates the plankton, resulting in bioluminescence. The response of the fish to the light flash is species-distinctive and allows the trained observer to make an estimation of species. The level of bioluminescent plankton organisms, the schooling configurations, depth of school, and composition of the school (mixed species), are some of the variables in night identification.

School size estimation.—The probability of sighting, identifying, and estimating school size, is affected by the training and ability of the spotter pilot. It was recognized in the beginning of the program that variation in estimating school size probably has more effect on the data than other variables. Some spotter pilots consistently report greater tonnages than do others (Squire 1972). Six of the fish-spotter pilots have continued full-time with the program since 1963 and were the major contributors. Therefore, if biases in reporting of tonnage were present, it may have been relatively consistent throughout the period. MacCall,[3] in an investigation of aerial spotter variation in reported abundance of anchovies, found that differences in spotting power appeared to be consistent for both day and night conditions for two periods of time (1 ½ yr apart). He also stated that variability in reported tonnages was high even for consecutive flights, giving wide confidence intervals of estimates of spotting power and daily fish abundance. A long-term averaging, however, will reduce the variance in estimates of mean abundance. In evaluating comparative observations between pilots as presented in the flight log, we do not know if they were looking at the same school or school group at the same time. If they were observing the same school or school group, it is possible that some period of time may have elapsed between observations, and the availability level changed. Estimation values between pilots may also change by species, requiring corrective factors by pilot for each species. For example, the anchovy is sometimes one of the more difficult species to evaluate and estimate tonnage because of the large school groups and large tonnages available.

Pilot estimation values for anchovy were calculated using data for the period 15 September to 31 December 1966, 1969, 1974, 1976, and 1977. Flight logs of two or more spotter pilots were compared, using observations thought to be near the same geographical location, for either day or night. One aerial spotter, recognized among his peers as an able and competent observer, was selected as the key observer and his observations were used as a reference base. The results for observations for other spotter pilots indicate that, when compared with the key aerial spotter, two pilots were estimating nearly the same as the key pilot, three were 0.4 times his estimate, two were 0.45 times, and three about 0.08 times. The differences in spotting power appeared to be consistent both day and night, as found by MacCall (footnote 3).

Aerial spotter pilots tended to survey portions of the ocean near their bases of operation: either the greater Los Angeles area or the Santa Barbara coastal area. Pilots operating in the same area tended to estimate the available tonnage in similar amounts, for they frequently communicated via radio and tended to cooperate in the searching and fishing operations in their respective search and fishing areas. As indicated previously, no effort was made during the period of the survey to attempt to influence the individual aerial spotter's tonnage estimation values and the major contributors to the program have participated throughout its 16-yr period.

Comparison of Apparent Abundance Measuring Techniques

A precise measure of a specie's total abundance and its biological composition is most desirable for the management of pelagic marine species. However, at the present time a precise measure of abundance is not possible. Management must therefore rely on sampling techniques to obtain a reasonable estimate of abundance and biological composition. The major coastal pelagic resources are conveniently being measured by methods of sampling which provide a measure or index of apparent abundance (catch or observations per effort). Larval surveys provide an apparent abundance measure, and acoustical surveys are conducted to determine the apparent abundance of fish schools. These apparent abundance indices are then adjusted to yield an estimate of total abundance. For the years since the start of the aerial survey program, some data are available giving estimates for Pacific mackerel and northern anchovy. These data can be compared with the trend of the aerial apparent abundance index. Three types of independent survey data are available for comparison: the larval survey, acoustical or sonar surveys, and the aerial spotter surveys. For the following species, some comparative data are available.

Pacific Mackerel

Smith and Richardson (1977) presented a graph of three independent estimates of the abundance of Pacific mackerel (Fig. 62) using three index values: spawning biomass, larval index, and aerial index. The aerial index can only be compared with values obtained after the start of the aerial survey in 1963. A rank correlation test (Spearman) was used to examine the aerial index vs. spawning biomass (1963-67), giving a significant correlation ($r_s = 1.00$). For the aerial index vs. larval index comparison, the correlation coefficient was $r_s = 0.77$, not significant at the 0.05 level. Although the statistics show promising results, it should be noted that the data are limited by the number of years tested, and that the three indices show a common decrease in value.

Northern Anchovy

Three research programs using different techniques have independently developed apparent abundance data concerning the anchovy resource. Larval catch data have been summarized to produce a larval index and an estimate of spawning biomass. Acoustical surveys to measure school number and size have been used to develop an acoustical index and an estimate of biomass. Aerial survey data have been used to develop an index of apparent abundance. The larval and acoustical techniques sometimes used different indices through the years.

Since all estimates are independent of each other, an analysis was made to determine if these methods were estimating a common source. A description of the data sources for Figure 63 is as follows: larval abundance data for the central subpopulation for 1963 through 1972 was provided by Smith,[4] and data from 1972 through 1978 by Stauffer (1980). Acoustical surveys have been conducted since 1966, but acoustical techniques were changed in 1971. Therefore, acoustical data were compiled from Mais (1974, footnote 5). Aerial survey data taken off the coasts of southern California and northwestern Baja California, Mexico, from published records 1962-69 (Squire 1972), and records through 1978 included in this publication, are in Table 2. Figure 63 shows the larval index from 1963 to 1978, for the central subpopulation, the aerial night index, and acoustical index. The acoustical index is based on $N \times 10^3$ schools for the early years, and the school's surface area (square nautical miles) for the later years. The larval index uses the estimated abundance of larvae $\times 10^{12}$ for the central subpopulation.

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[3] MacCall, A. 1975. Investigation of aerial spotter variation in reported abundance of anchovies. Anchovy Workship Meeting, July 21-22, 1975, contrib. 19, 3 p. Southwest Fisheries Center La Jolla Laboratory, NMFS, NOAA, La Jolla, CA 92038

[4] P. E. Smith, Fishery Research Biologist, Southwest Fisheries Center La Jolla Laboratory, NMFS, NOAA, La Jolla, CA 92038, pers. commun. 1974

[5] Mais, K. F. 1978. Acoustic survey for the assessment of anchovy resources off California and northern Baja California. Unpubl. manuscr., 21 p. California Department of Fish and Game, Marine Resources Laboratory, 350 Golden Shore, Long Beach, CA 90802

Significant Spearman rank correlations were not found for comparison of aerial to larval and acoustical survey data for 1963-72. Comparison of aerial and acoustical survey indices for the period 1972-78 gave a significant correlation ($r_s = 0.810$, $P = 0.05$). During this period, only three larval surveys were conducted, not an adequate sample for calculating a correlation. MacCall et al. (1976) calculated a correlation coefficient of +0.30 for larvae vs. aerial (night) surveys during 1962-66, and for 1968 and 1969. More recently, an anchovy spawning biomass estimate based on egg production has been developed (MacCall et al. 1982). The correlation between the aerial (night) anchovy index with the new biomass estimate is very high (Fig. 64).

The aerial night index appears to be closely correlated with the acoustical index developed during the years since 1971. Larval surveys cover a larger geographical area than either the aerial or acoustical surveys, generally extending further offshore. The aerial survey involves only the nearshore area where the purse seine fishery operates. This area commonly has large concentrations of near-surface schooling fish and suitable sea-state conditions for purse seining, conditions which are not common in the offshore areas.

The anchovy night aerial abundance index was not unusually high during the first years of the surveys compared with levels observed in 1973-76. The aerial surveys were started about the time the anchovy population was reported by Ahlstrom (1968) to have reached a plateau in about 1962. The anchovy larvae index for the central subpopulation declined during 1965-72, increased slightly in 1975, then declined sharply in 1978 The aerial and sonar indices rose two or more times their former levels to high levels in 1973 and 1975, then declined, with the aerial index declining to slightly below pre-1972 levels.

The geographical area covered by the aerial survey program contained the major commercial fishing grounds. High abundance level indices from the aerial spotter data were not evident for this area, which apparently did not benefit from the high larval index levels that started in 1962 and resulted in population estimates of 4.0 to 5.0×10^6 t (Ahlstrom 1968). However, a significant but unexplained change to high aerial and acoustic index trends occurred in the fishery during 1973-75, prior to a rapid decline during 1976-78, in the larval, acoustical, and aerial indices.

Pacific Bonito

Studies have been made using the aerial day index of Pacific bonito observed off southern California, in correlation with recreational partyboat CPUE, using yearly time-lag periods (MacCall et al. 1976). The recreational fleet which fishes nearshore generally catches younger fish than the commercial purse seine fleet. The highest correlation between the recreational fleet CPUE and the aerial apparent abundance index for the commercial fishery was for a 3-yr lag period ($r = 0.69$) which is shown in Figure 65. We believe this correlation to be useful in predicting recruitment into the commercial fishery, based on partyboat CPUE.

SUMMARY

The aerial index data is positively correlated with the trend of other measures of apparent abundance, particularly the acoustical survey (post-1971) for anchovy abundance. For the limited amount of comparable data available, the Pacific mackerel aerial index appears to correlate well with the biomass estimates. The index levels of Pacific bonito, a species that is more common to the south, show trends that appear to parallel the trend of the biomass.

Index trends for both the northern anchovy, beginning in 1974, and Pacific bonito, in 1968 and 1973, show a pronounced downward slope one to two years before major declines occurred in these fisheries.

This program has used the available talents of commercial fish spotters who use standard visual techniques to observe pelagic schooling fish. In recent years, airborne electronic surveillance systems specifically designed to measure the extent of the available near-surface schooling resources at night have been developed. These new techniques, if used in close coordination with commercial operations and research studies, could produce for the program a more refined estimate of apparent abundance, not only for the fishing areas commonly surveyed by the commercial spotters but also for areas farther offshore where resources such as the anchovy are commonly observed during the winter-spring spawning season.

All analyses to date have involved only the production of basic apparent abundance indices, and have not been further adjusted to produce a more refined index or estimates of biomass. The aerial apparent abundance data should be further analyzed to provide more refined estimates of abundance for the major pelagic species. Studies are currently in progress to do this.

ACKNOWLEDGMENTS

The cooperation and interest of the commercial aerial fish spotters over a period of 16 yr is sincerely appreciated by the author. Spotter pilots who participated in the program are some of the best talents in the profession: John Bourgois, C. L. Devillier, Ed Durden, Leon Durden, Jim Ferreri, Roger Hillhouse, Frank Iacono, Jack Mardesich, Paul Mardesich, Tony Marinkovich, Joe Miles, John O'Connor, Chuck Rogers, Jack Whalen, and Andy Witmer.

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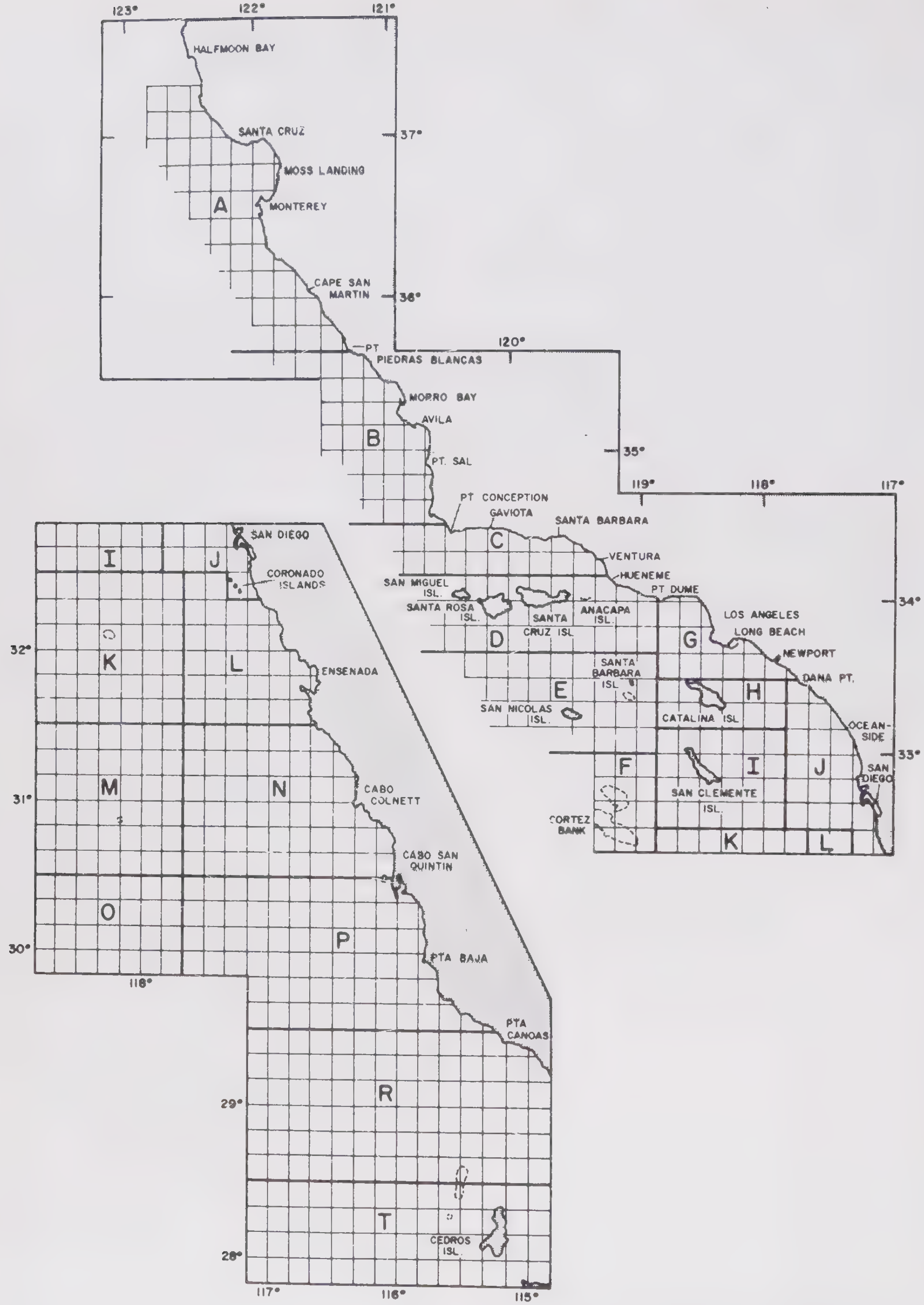

Figure 1.—Block areas from near Half Moon Bay, Calif., to Cedros Island, Baja California, Mexico, grouped in zones A to T as used in this study.

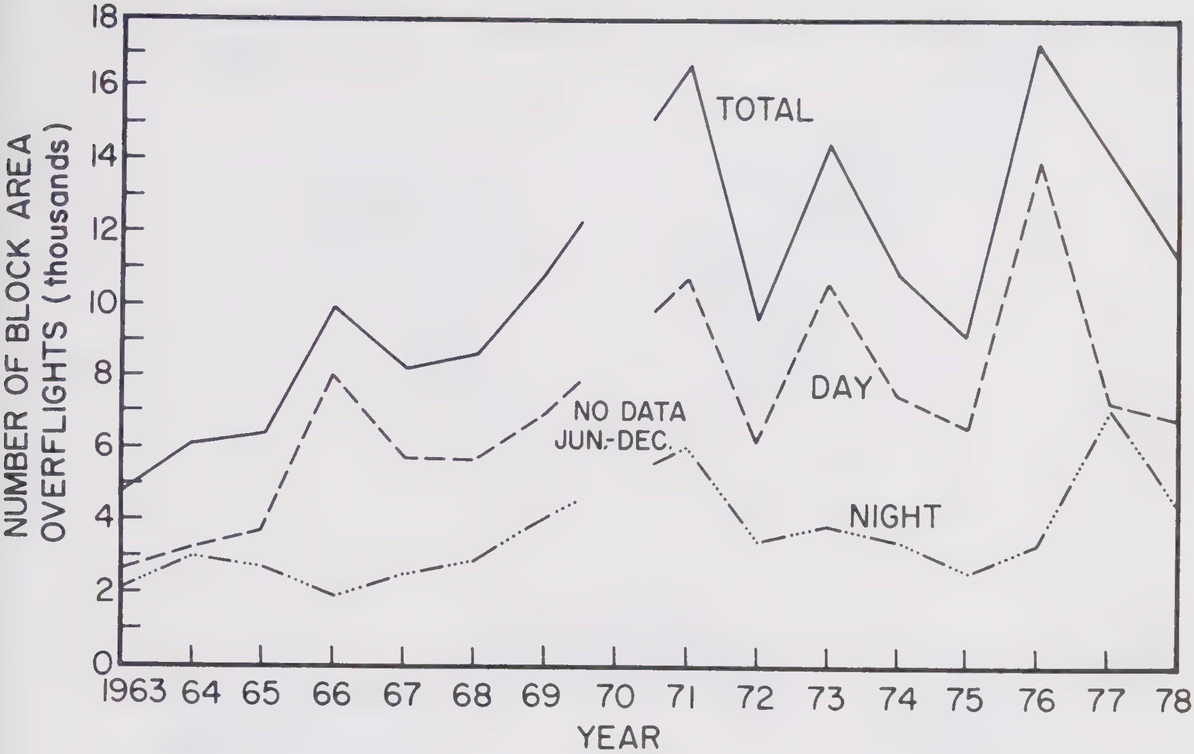

Figure 2.—Summary of observation effort, 1962-78, in terms of total day, night, and total overflights of block areas.

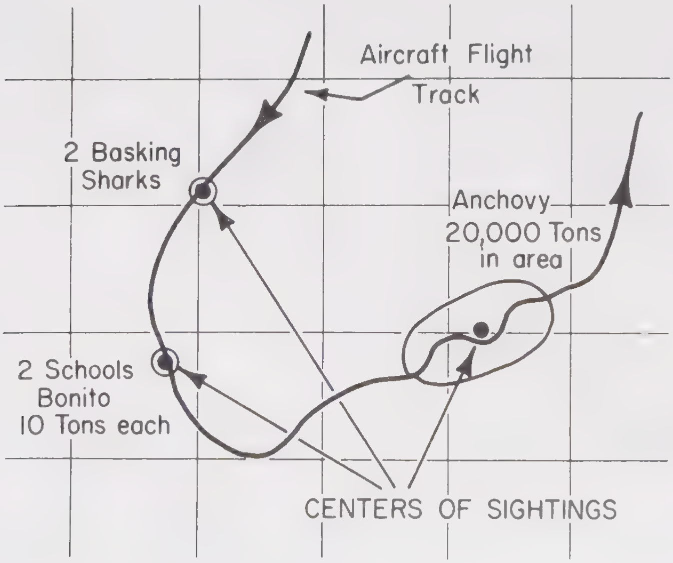

Figure 3.—Graphic description of positioning the center of sighting.

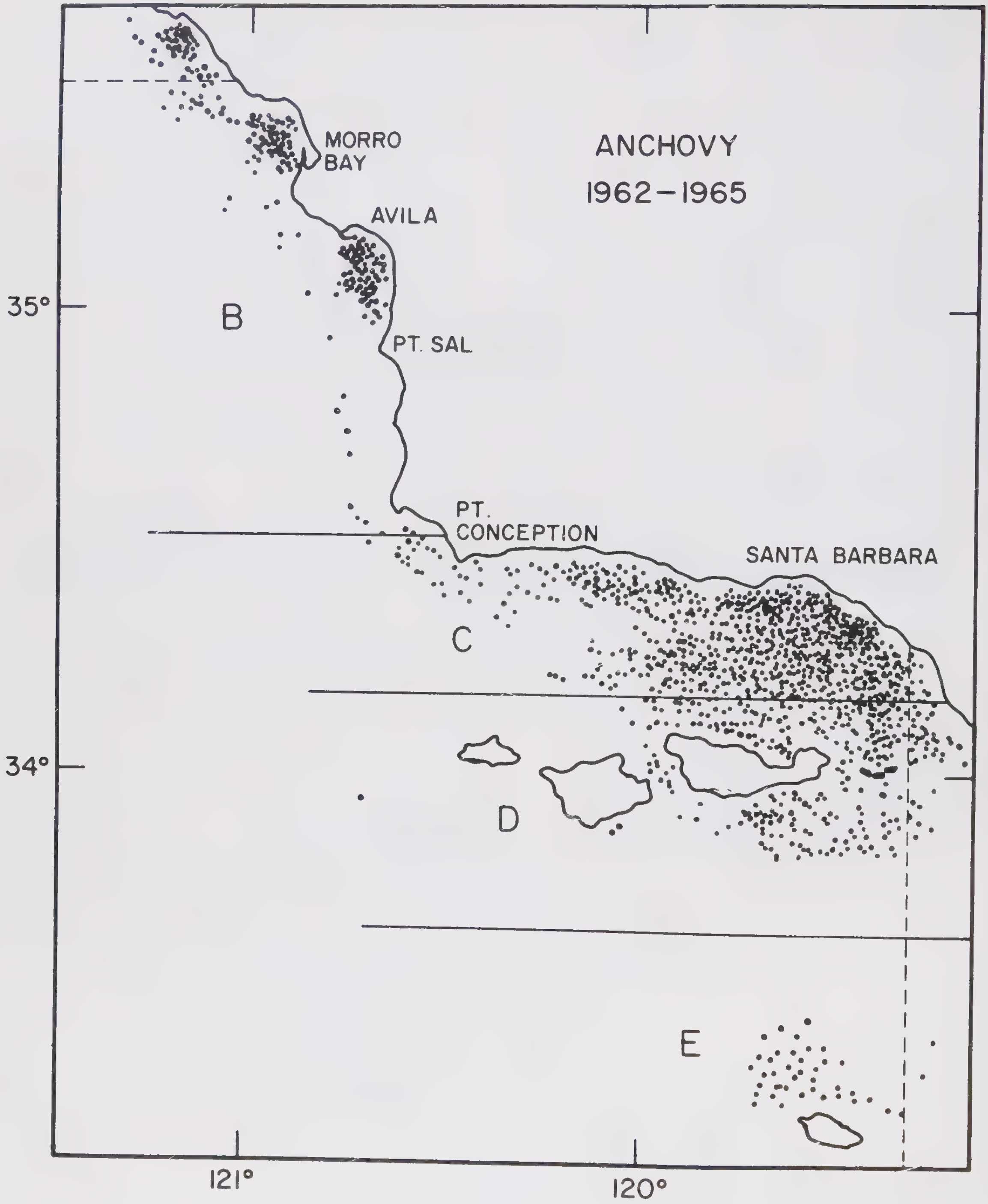

Figure 4.—Northern anchovy—location of centers of sighting for school or school groups, Morro Bay to San Nicolas Island, 1962-65.

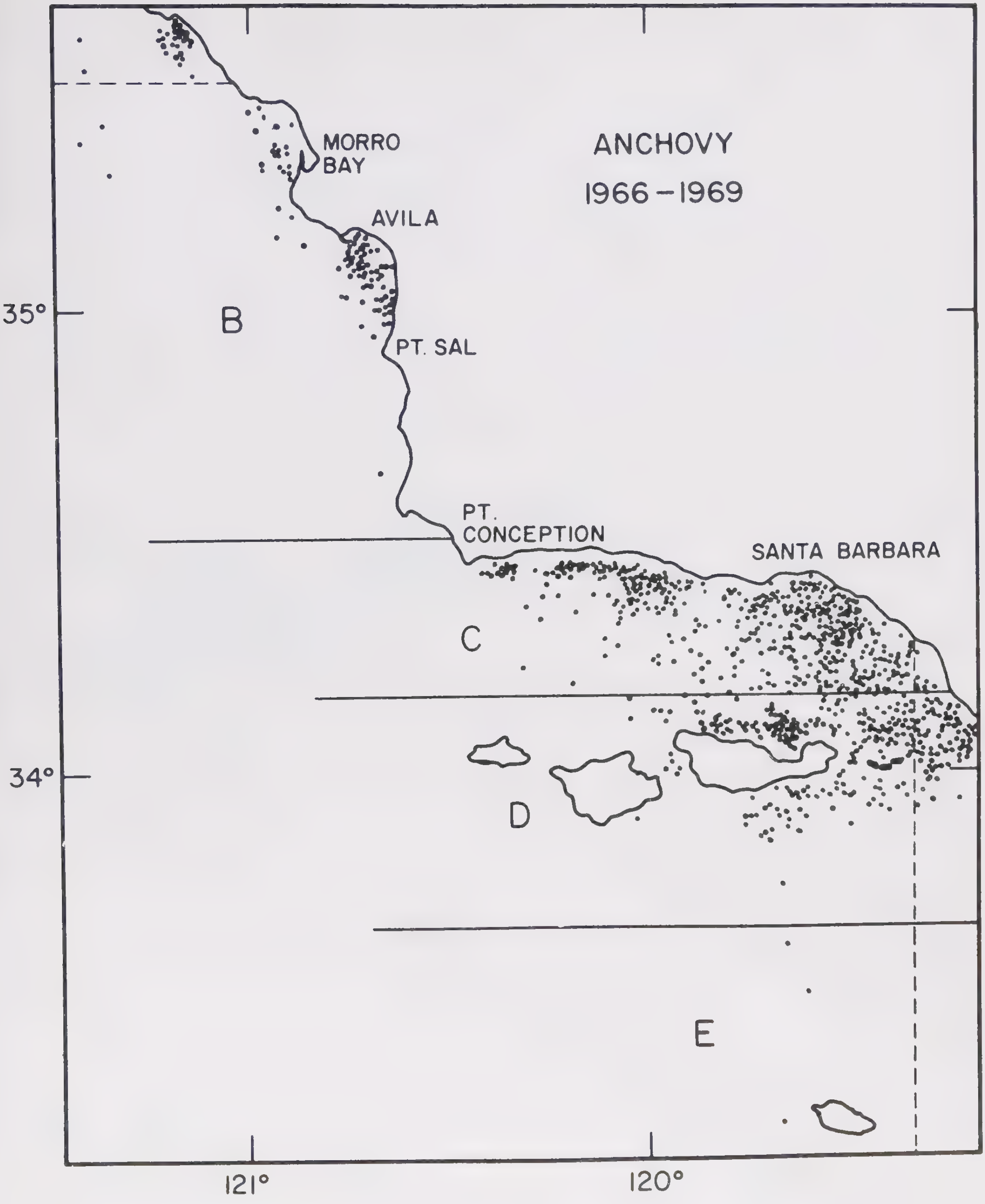

Figure 5.—Northern anchovy—location of centers of sighting for school or school groups, Morro Bay to San Nicolas Island, 1966-69.

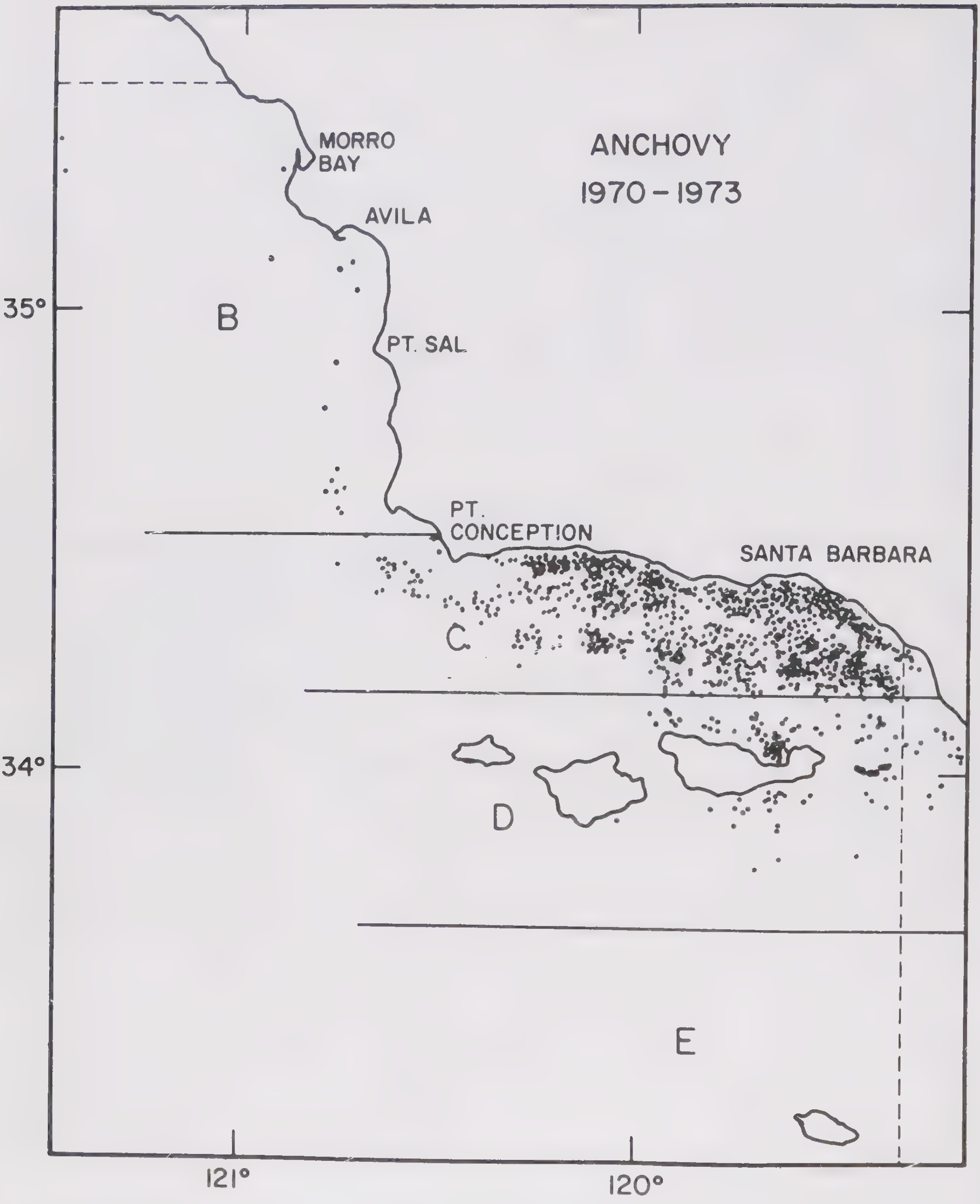

Figure 6.—Northern anchovy—location of centers of sighting for school or school groups, Morro Bay to San Nicolas Island, 1970-73.

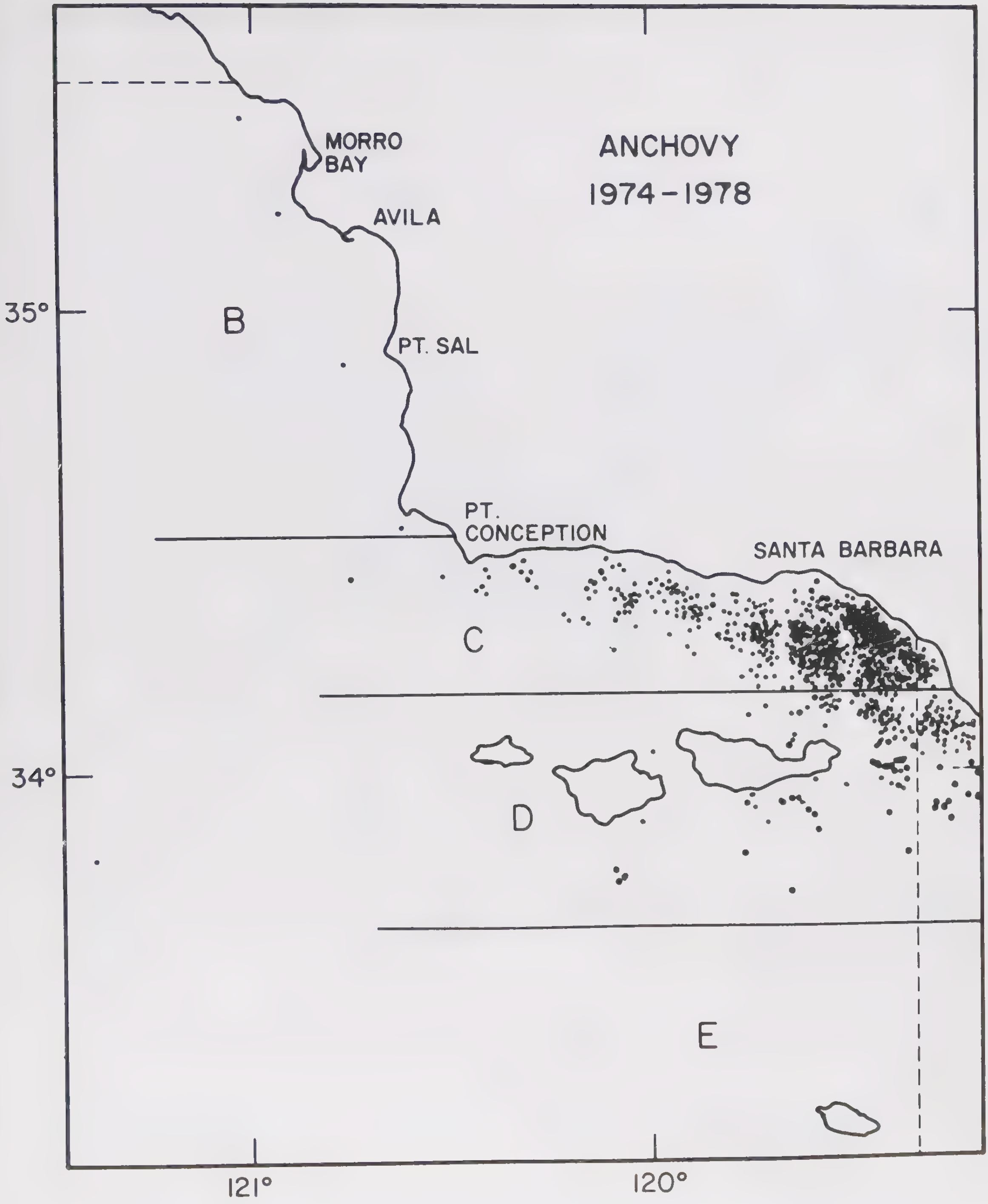

Figure 7.—Northern anchovy—location of centers of sighting for school or school groups, Morro Bay to San Nicolas Island, 1974-78.

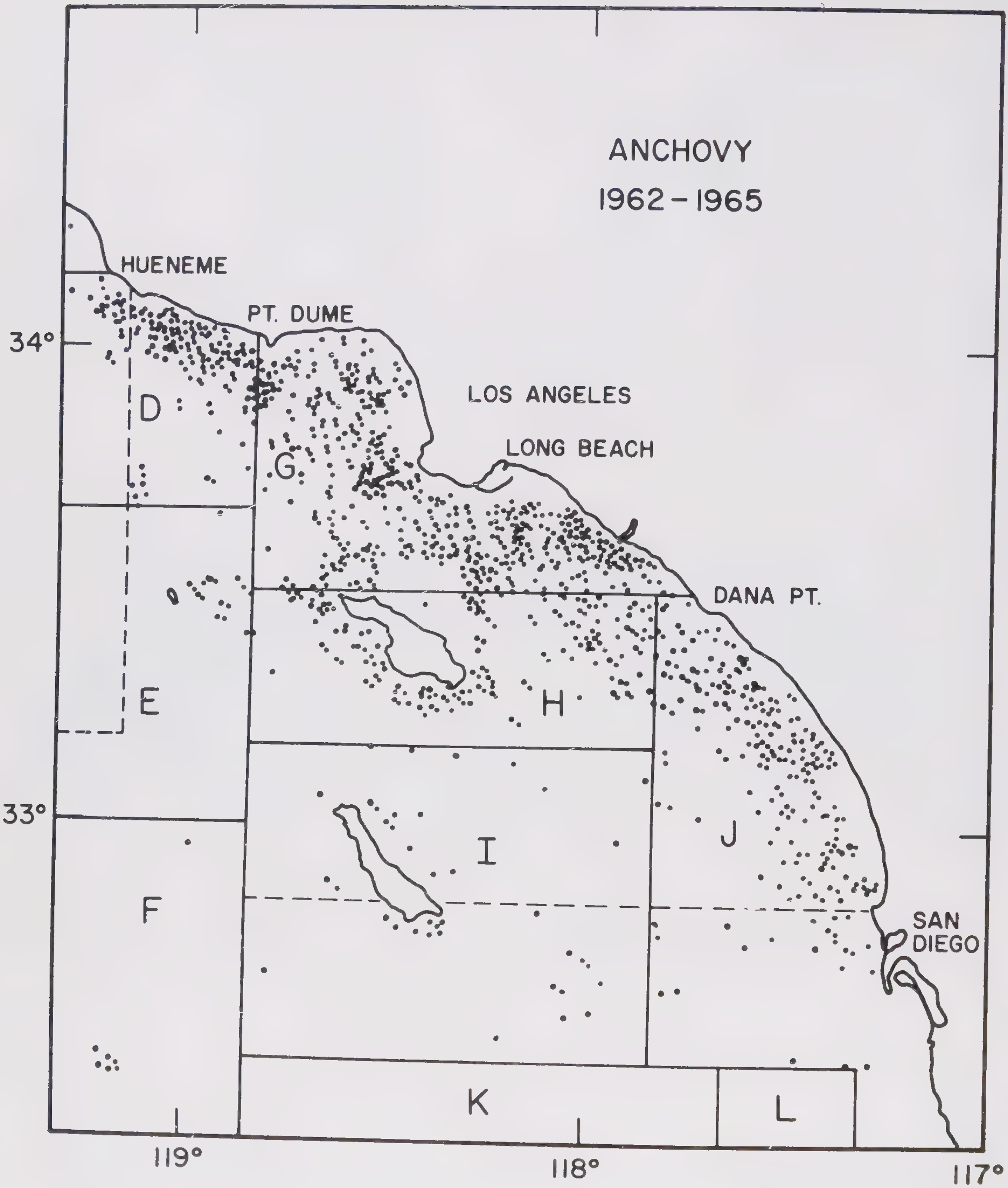

Figure 8.—Northern anchovy—location of centers of sighting for school or school groups, Pt. Hueneme to San Diego, 1962-65.

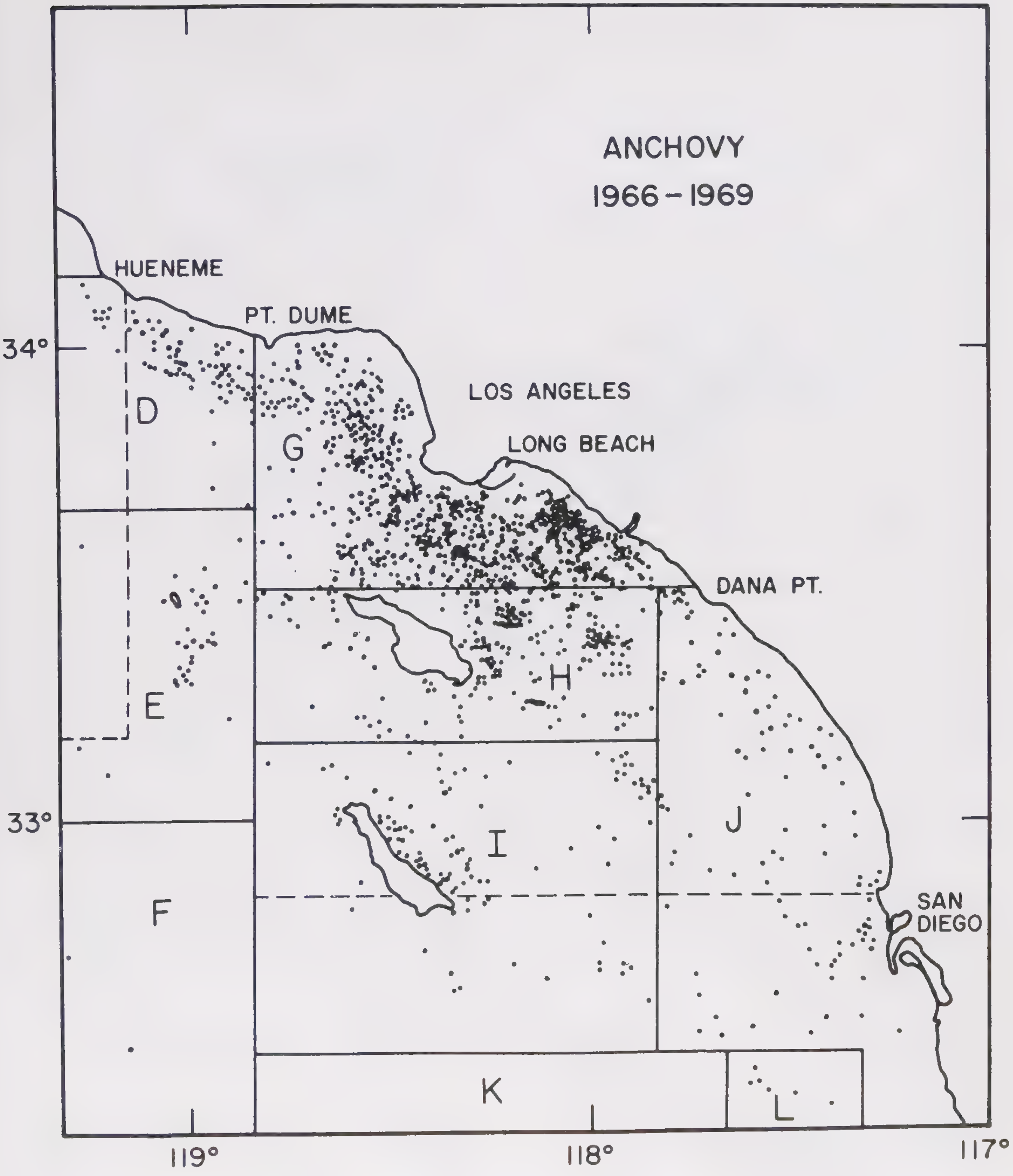

Figure 9.—Northern anchovy—location of centers of sighting for school or school groups, Pt. Hueneme to San Diego, 1966-69.

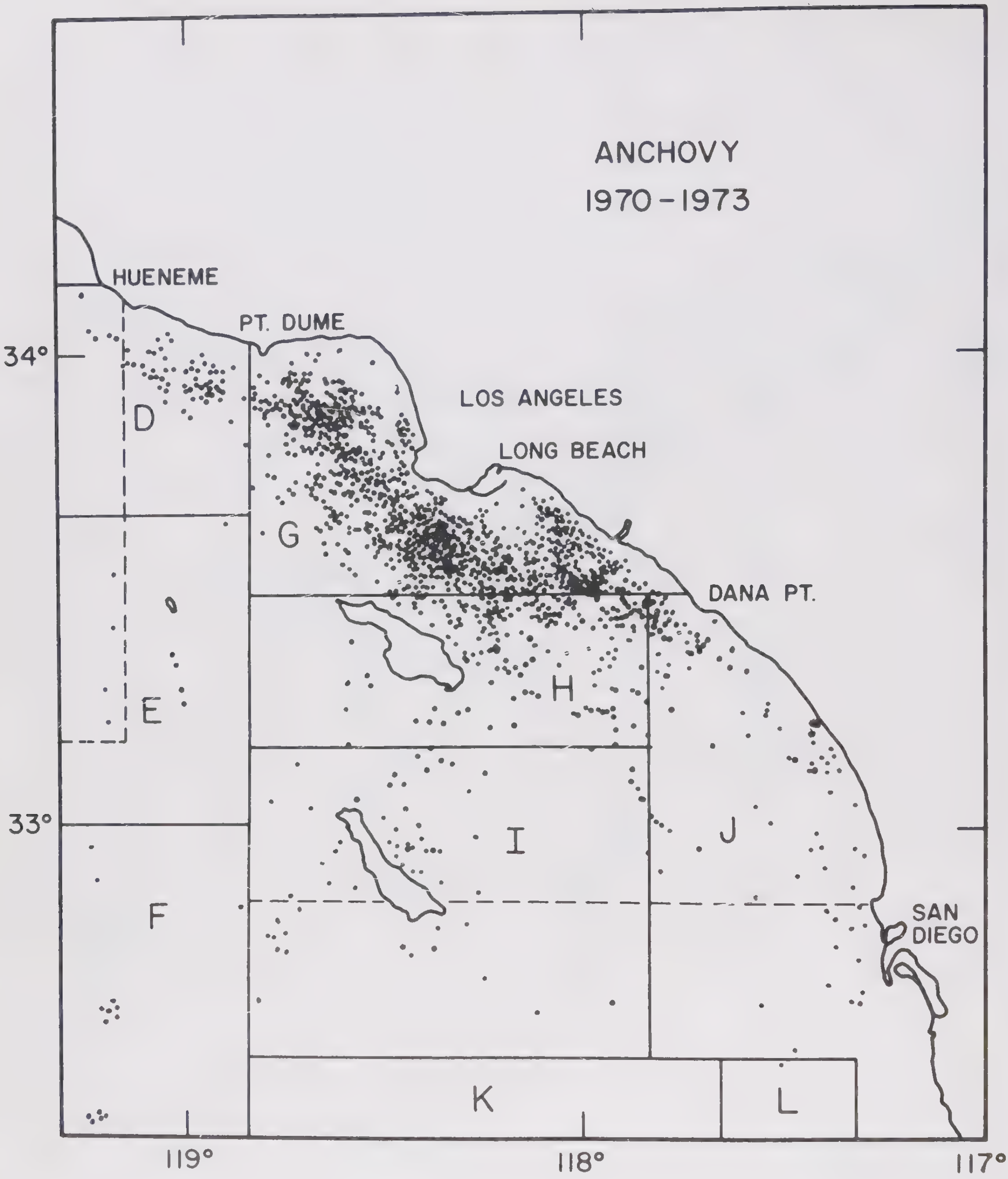

Figure 10.—Northern anchovy—location of centers of sighting for school or school groups, Pt. Hueneme to San Diego, 1970-73.

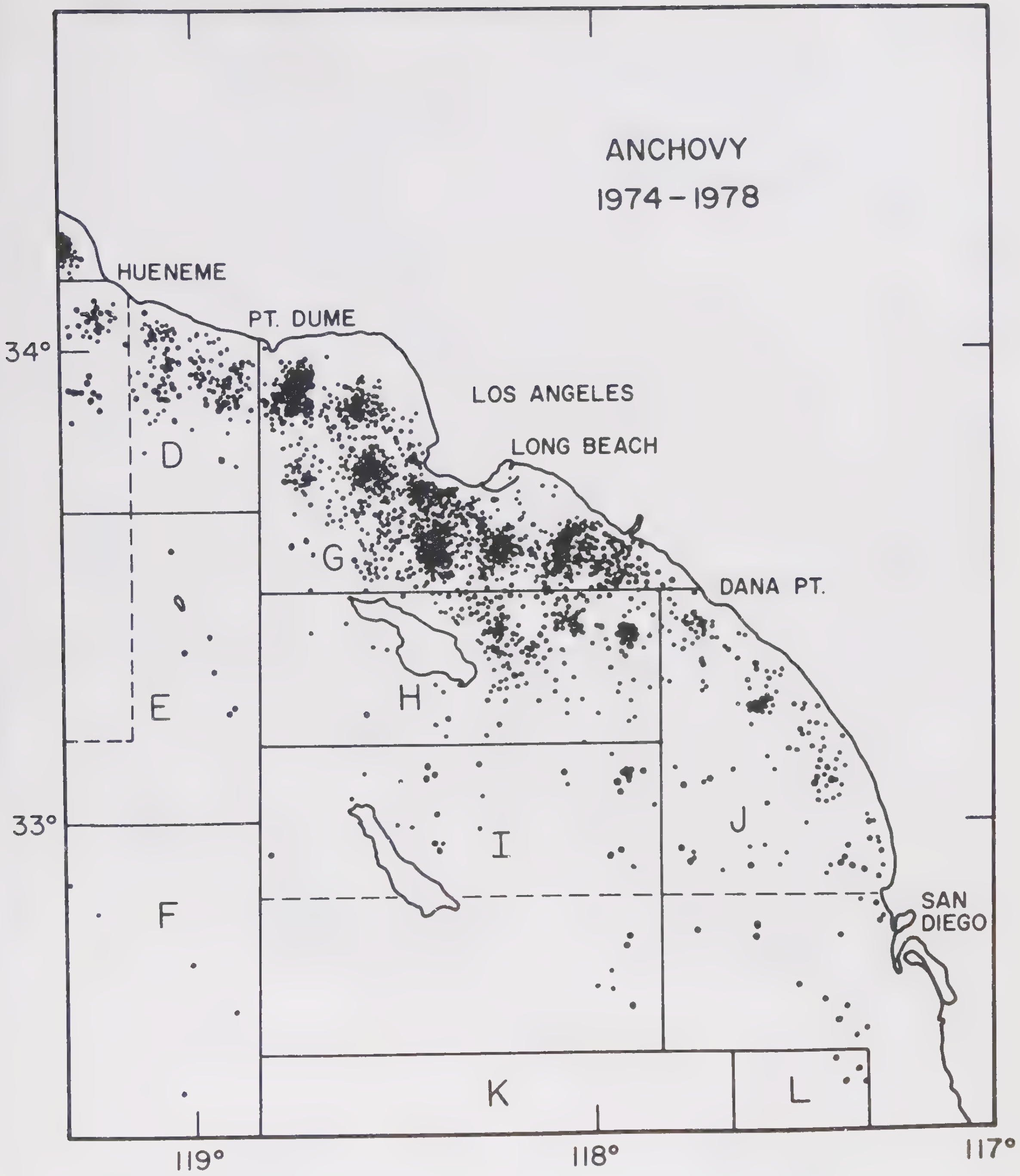

Figure 11.—Northern anchovy—location of centers of sighting for school or school groups, Pt. Hueneme to San Diego, 1974-78.

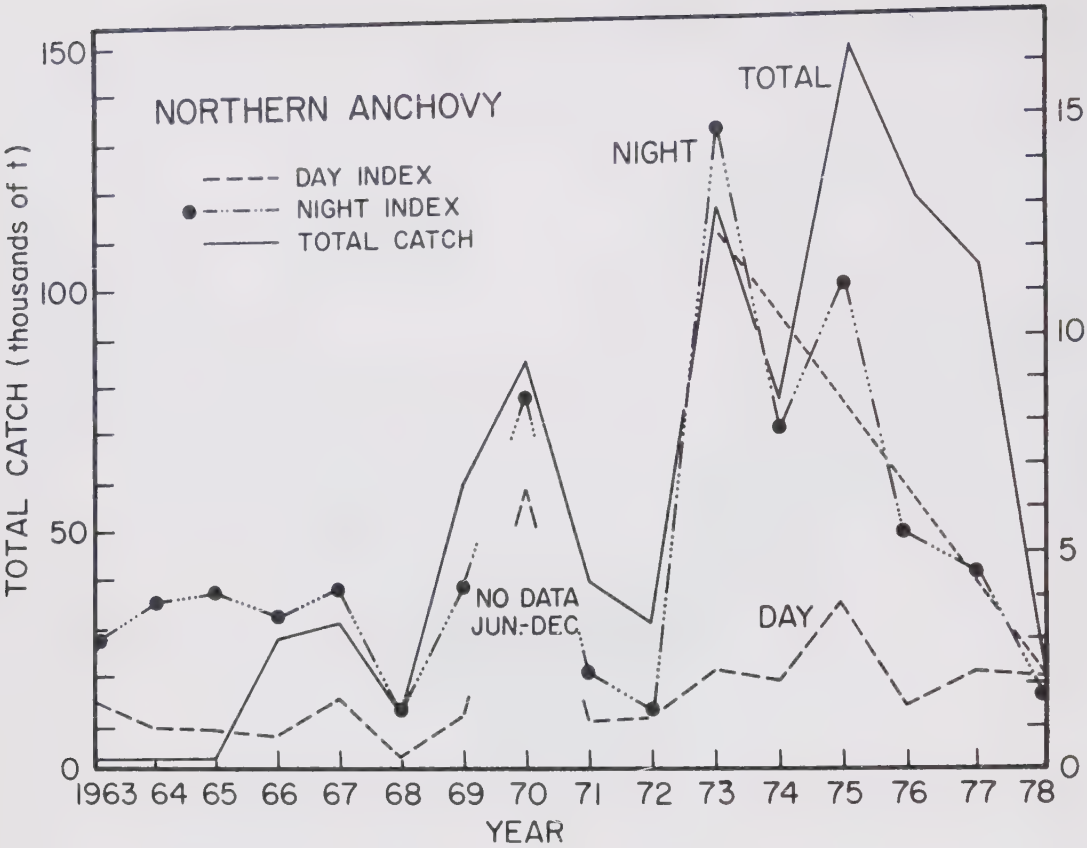

Figure 12.—Northern anchovy index values for day and night observations in arbitrary units and total California catch.

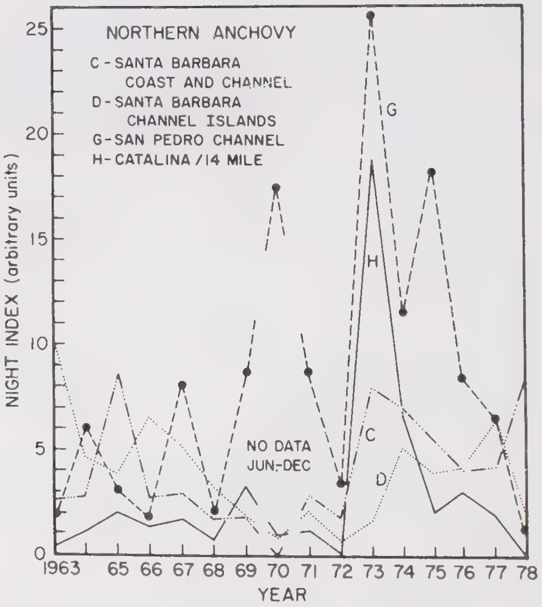

Figure 13.—Northern anchovy night index values in arbitrary units for the major fishing areas.

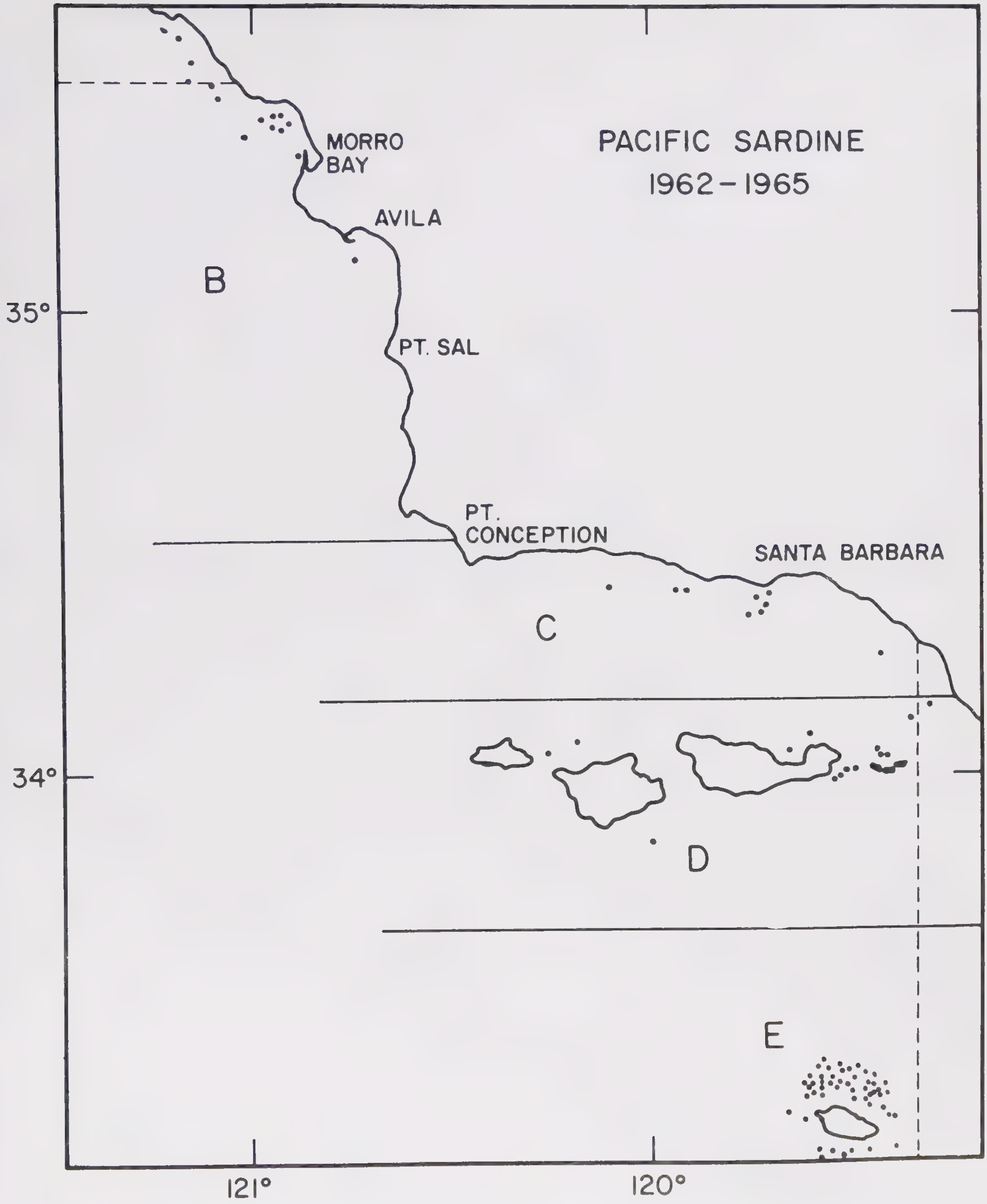

Figure 14.—Pacific sardine—location of centers of sighting for school or school groups, Morro Bay to San Nicolas Island, 1962-65.

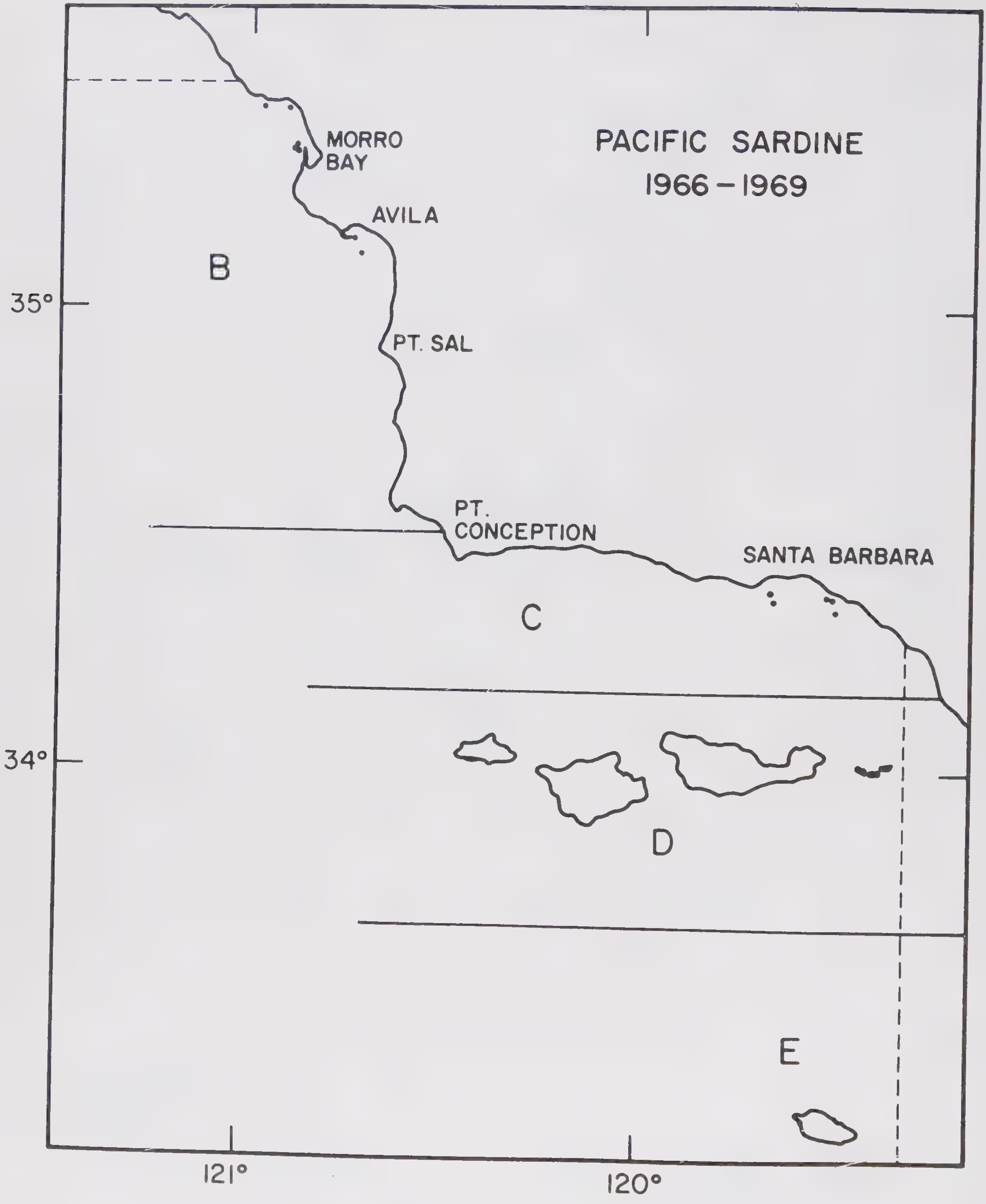

Figure 15.—Pacific sardine—location of centers of sighting for school or school groups, Morro Bay to San Nicolas Island, 1966-69.

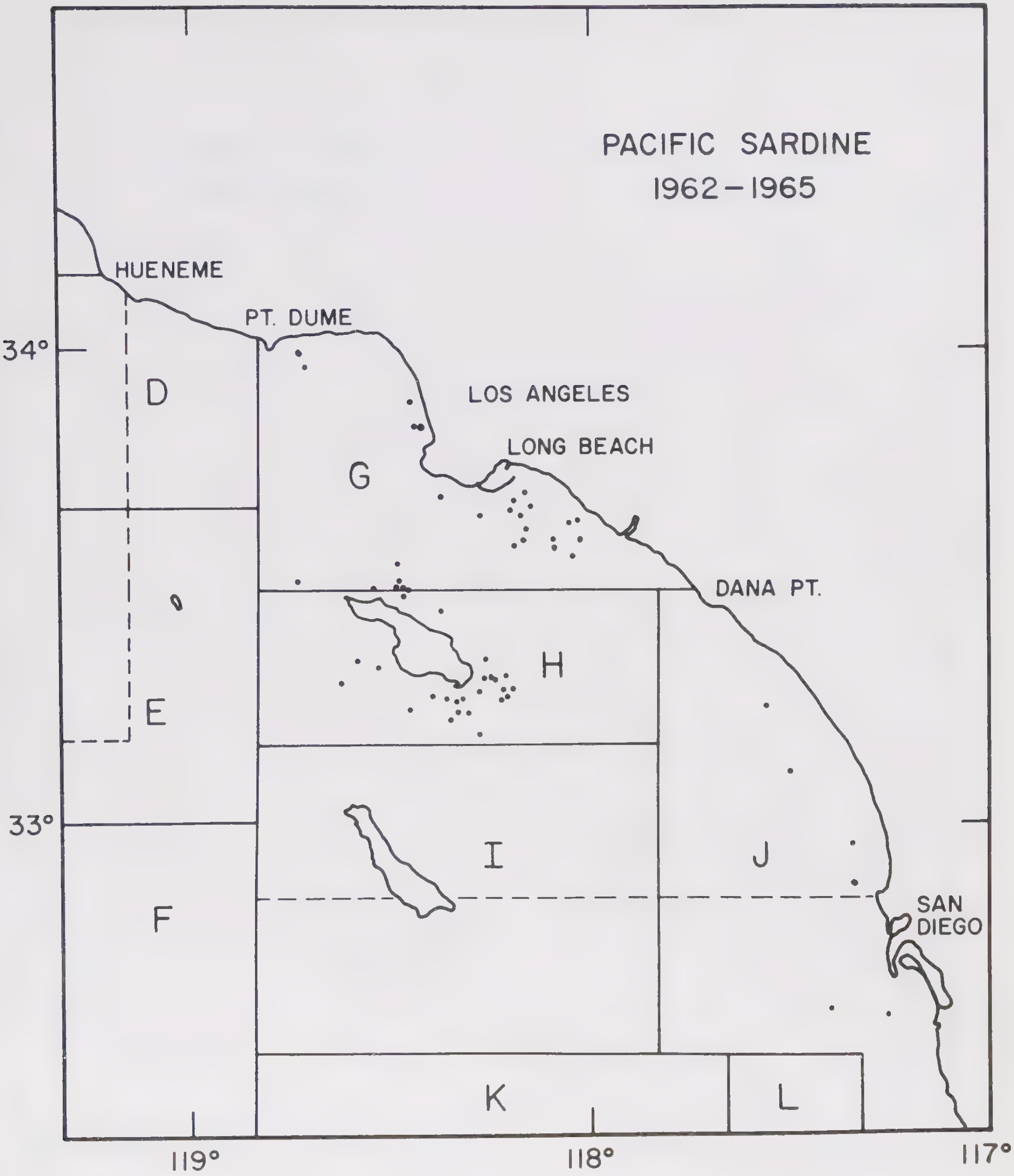

Figure 16.—Pacific sardine—location of centers of sighting for school or school groups, Pt. Hueneme to San Diego, 1962-65.

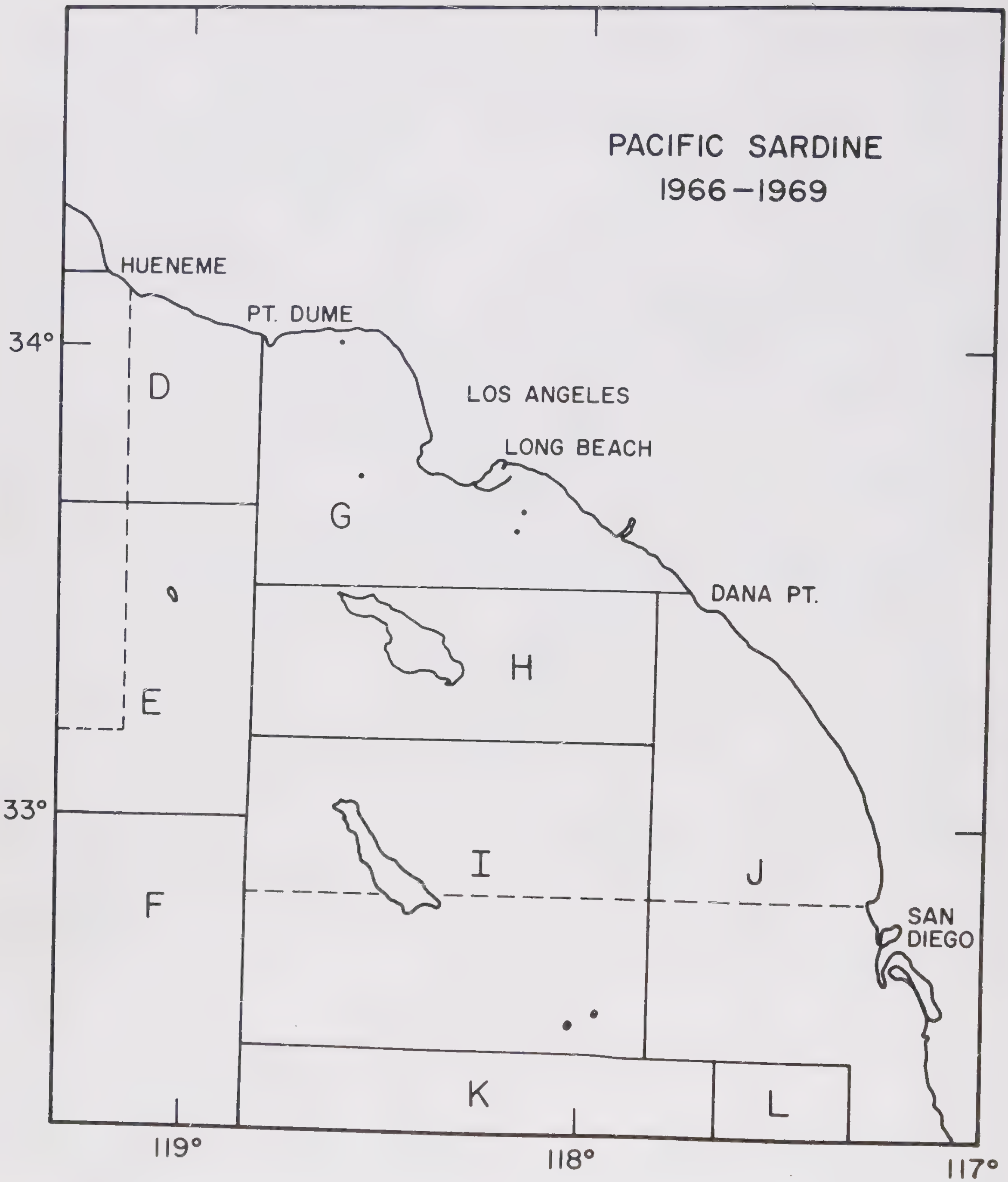

Figure 17.—Pacific sardine—location of centers of sighting for school or school groups, Pt. Hueneme to San Diego, 1966-69.

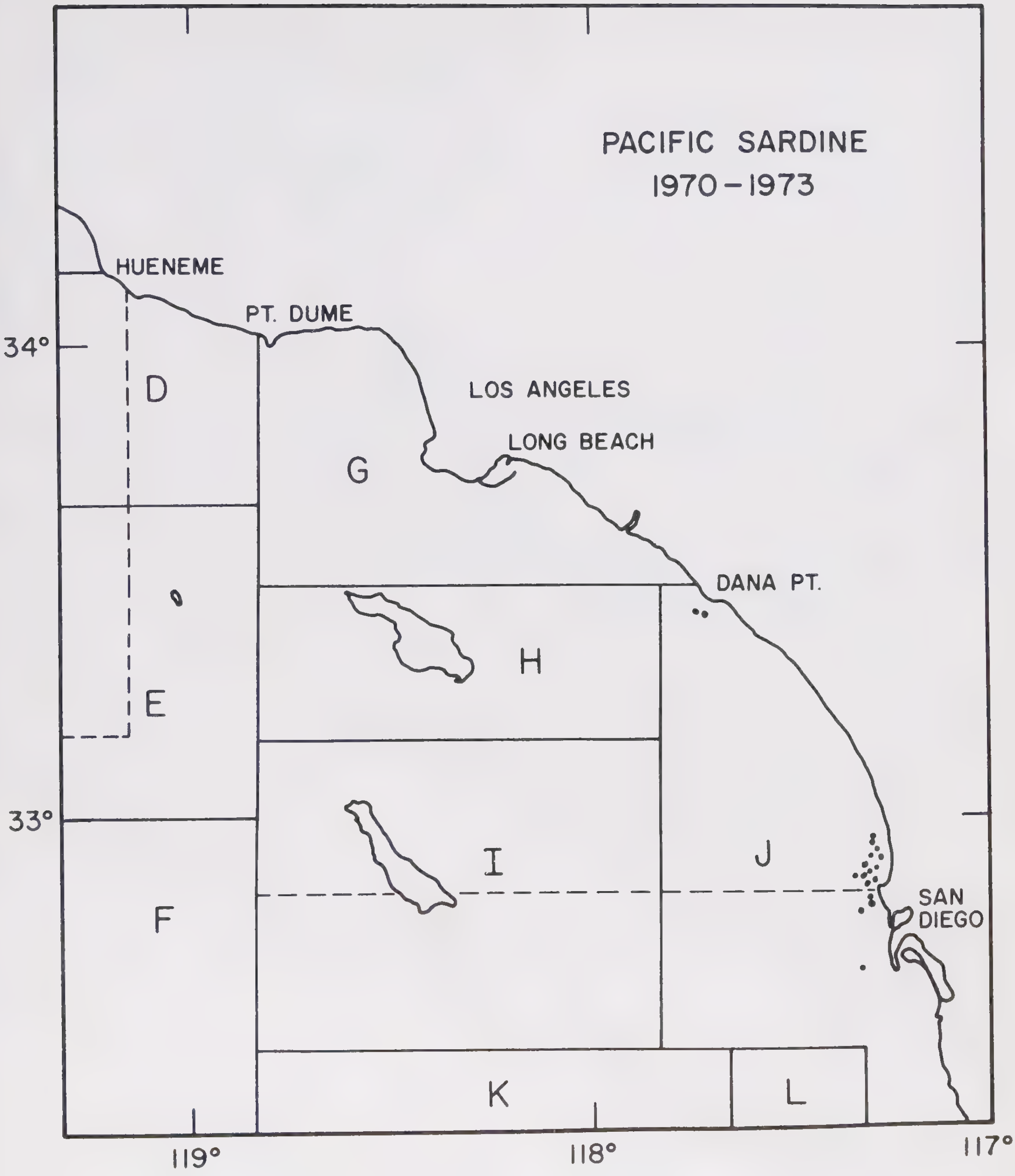

Figure 18.—Pacific sardine—location of centers of sighting for school or school groups, Pt. Hueneme to San Diego, 1970-73.

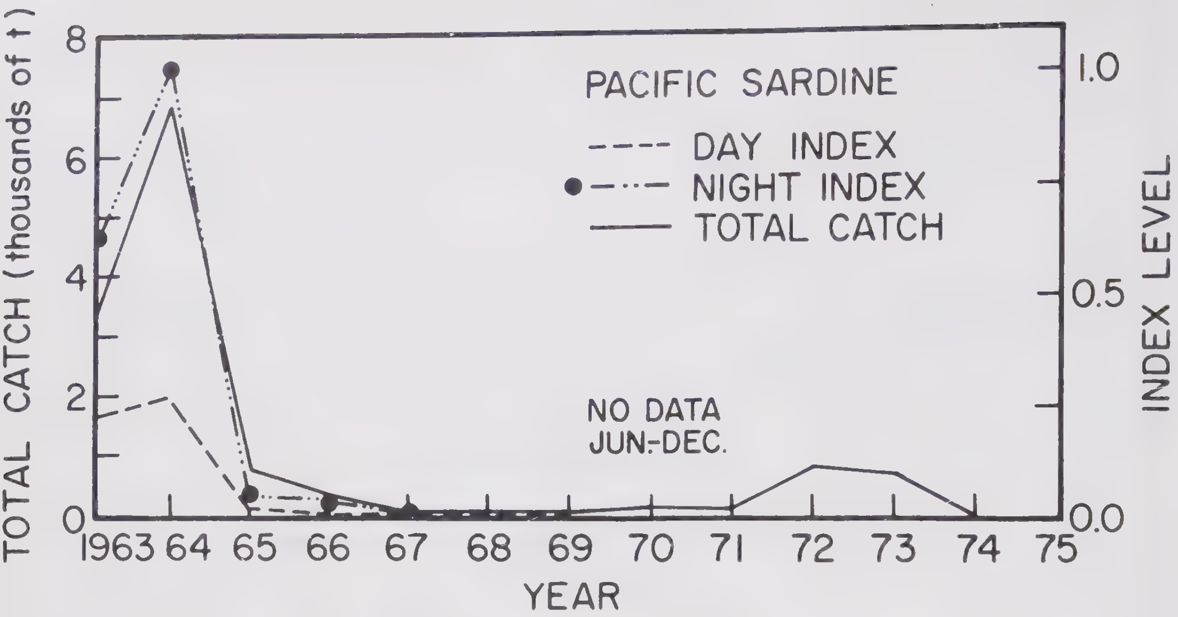

Figure 19.—Pacific sardine index values in arbitrary units for day and night observations and total California catch.

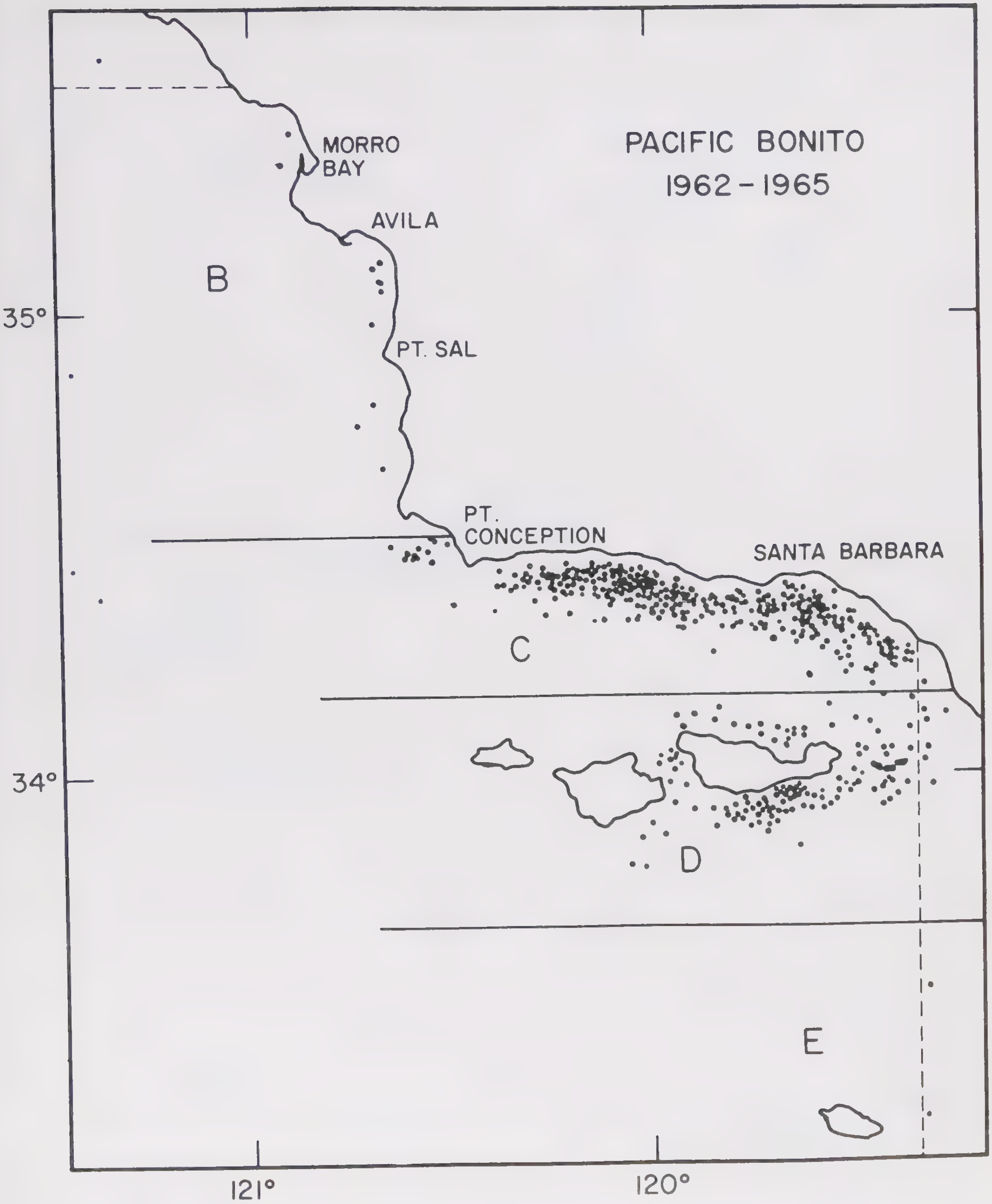

Figure 20.—Pacific bonito—location of centers of sighting for school or school groups, Morro Bay to San Nicolas Island, 1962-65.

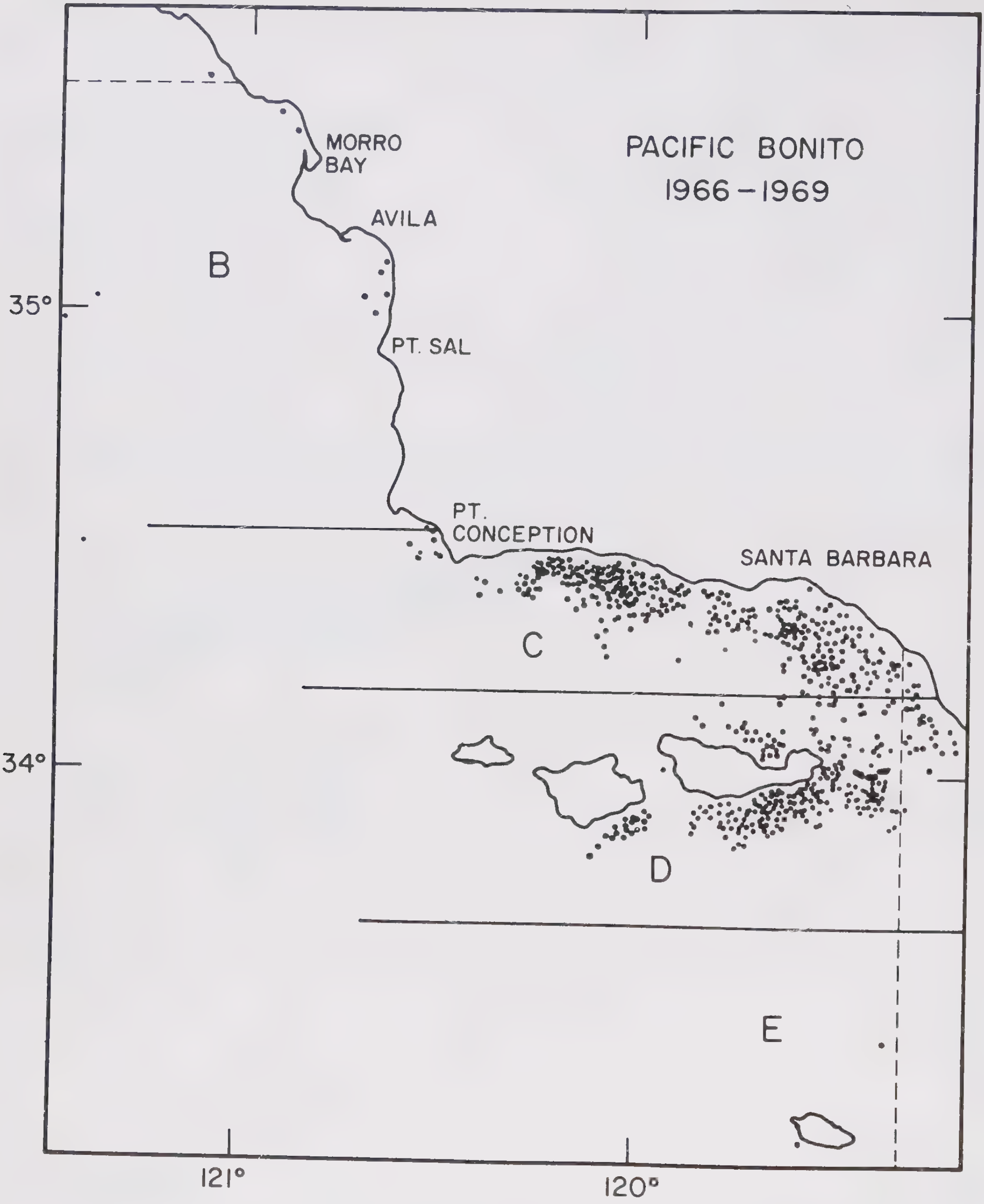

Figure 21.—Pacific bonito—location of centers of sighting for school or school groups, Morro Bay to San Nicolas Island, 1966-69.

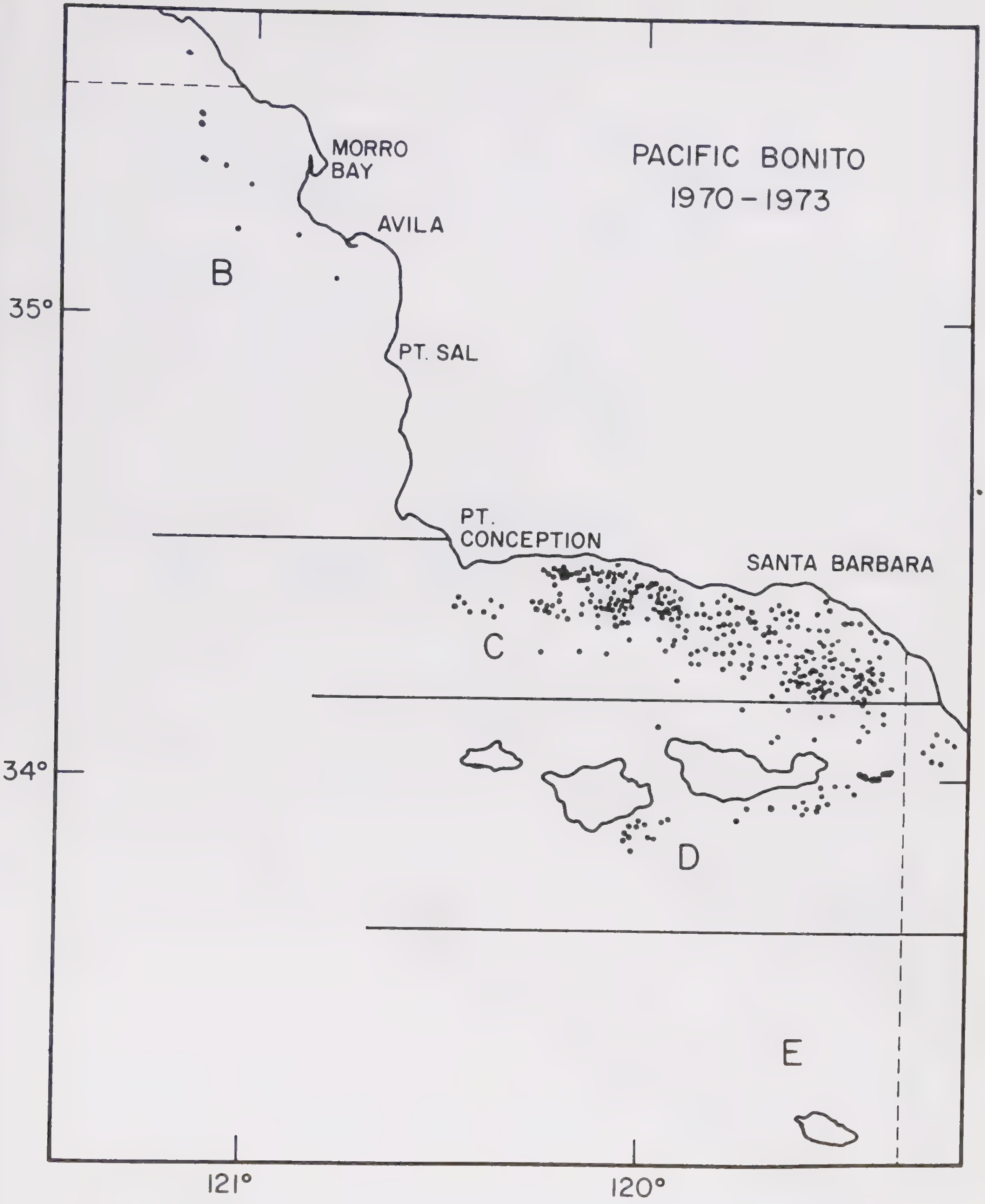

Figure 22.—Pacific bonito—location of centers of sighting for school or school groups, Morro Bay to San Nicolas Island, 1970-73.

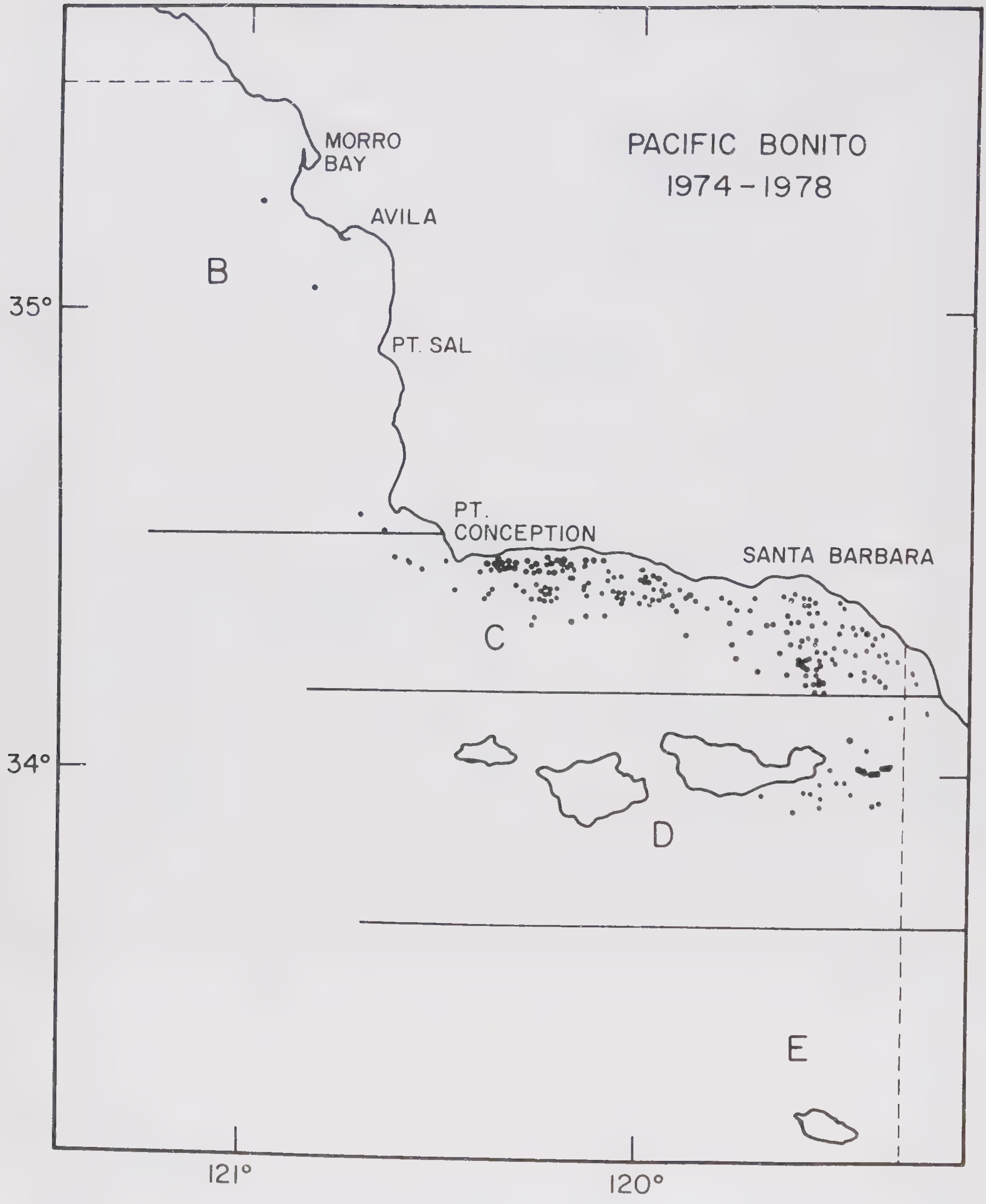

Figure 23.—Pacific bonito—location of centers of sighting for school or school groups, Morro Bay to San Nicolas Island, 1974-78.

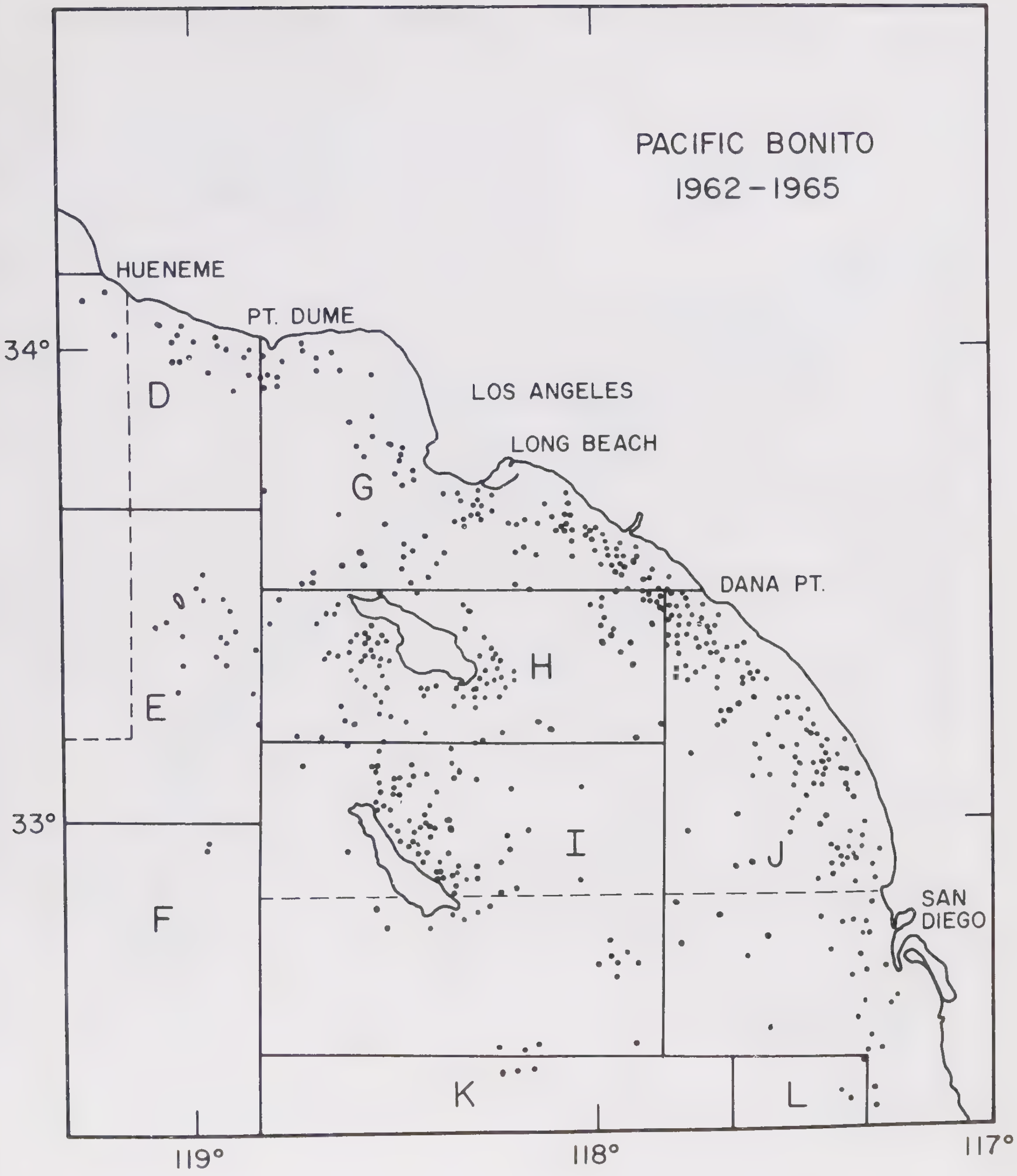

Figure 24.—Pacific bonito—location of centers of sighting for school or school groups, Pt. Hueneme to San Diego, 1962-65.

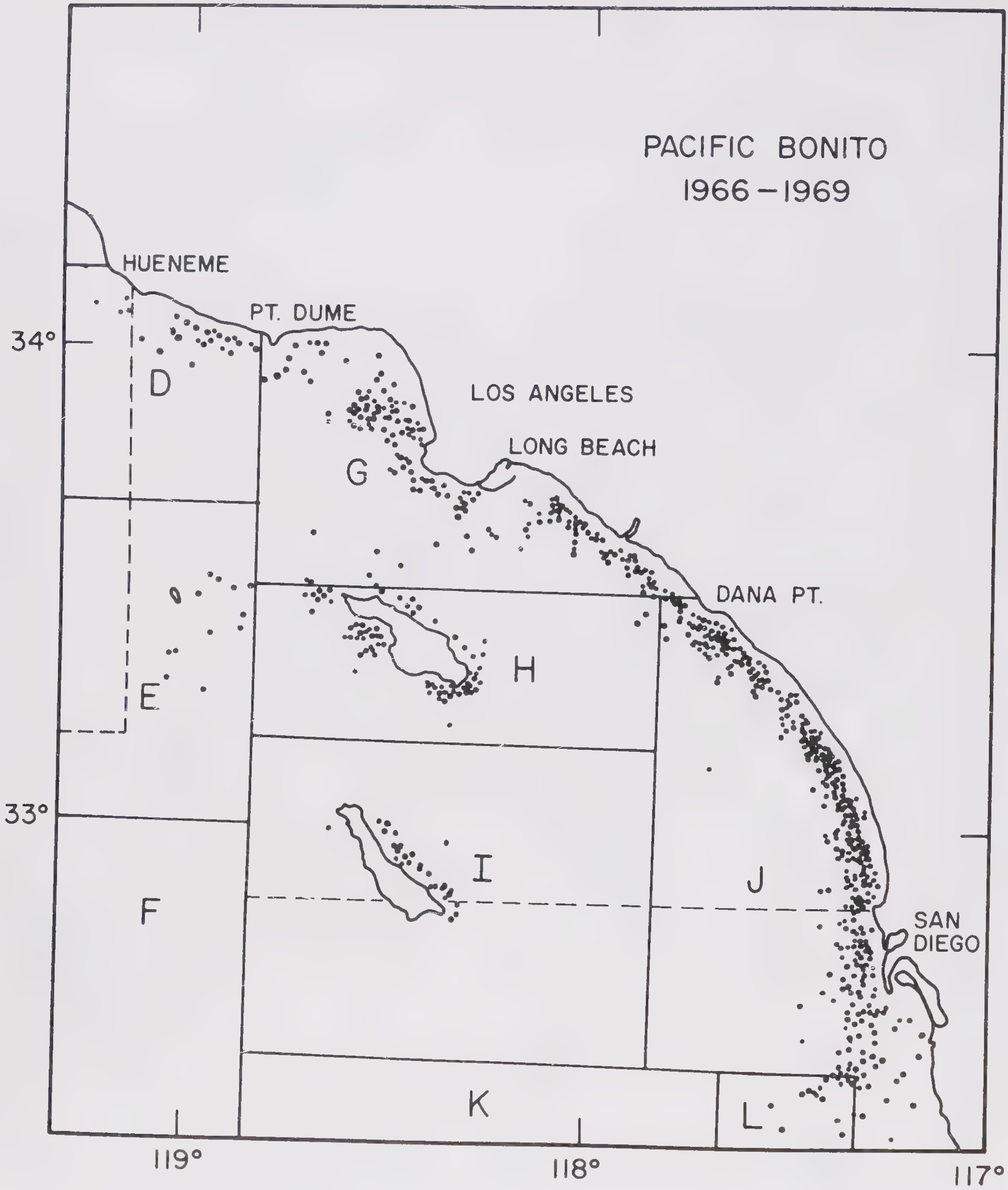

Figure 25.—Pacific bonito—location of centers of sighting for school or school groups, Pt. Hueneme to San Diego, 1966-69.

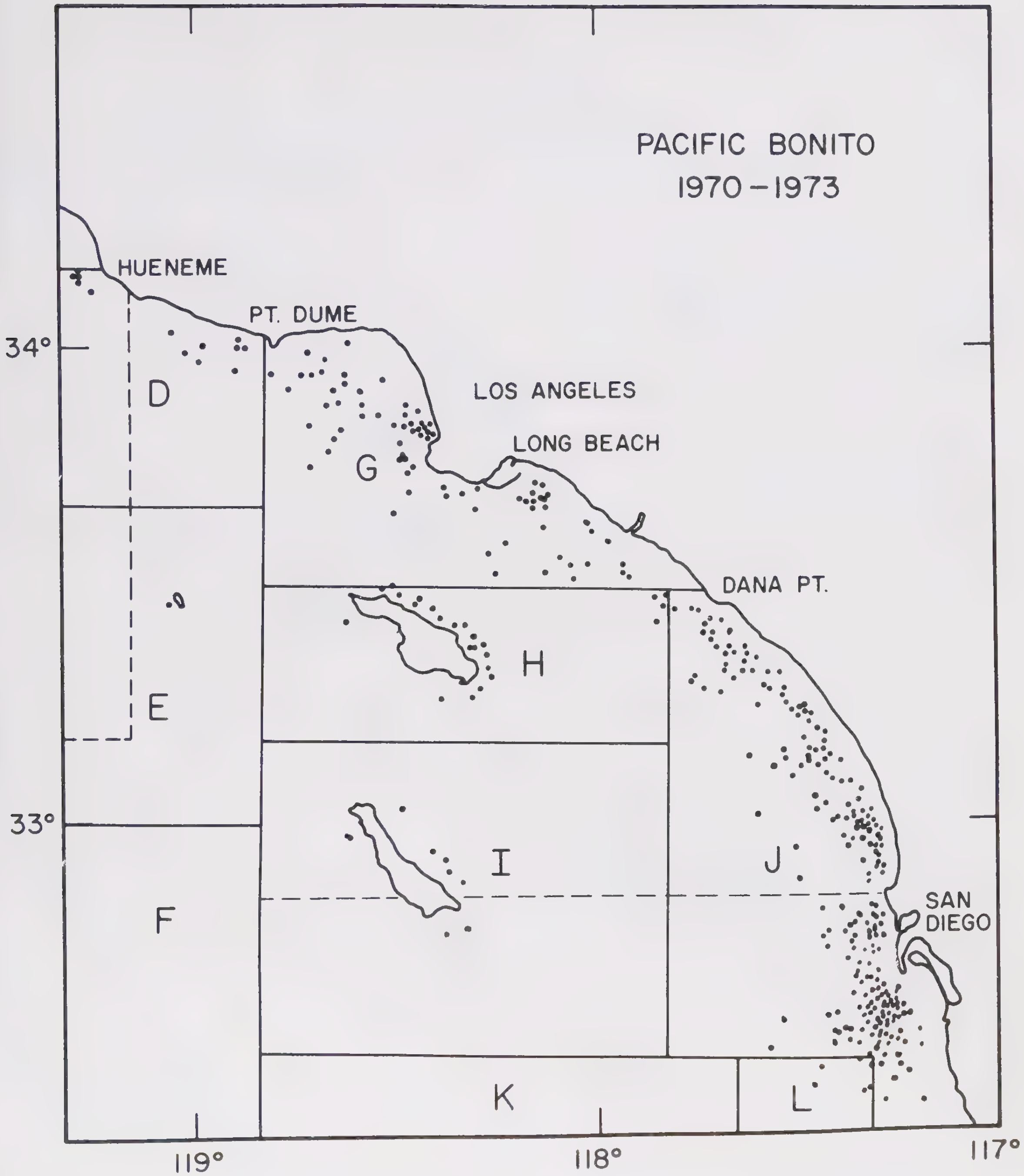

Figure 26.—Pacific bonito—location of centers of sighting for school or school groups, Pt. Hueneme to San Diego, 1970-73.

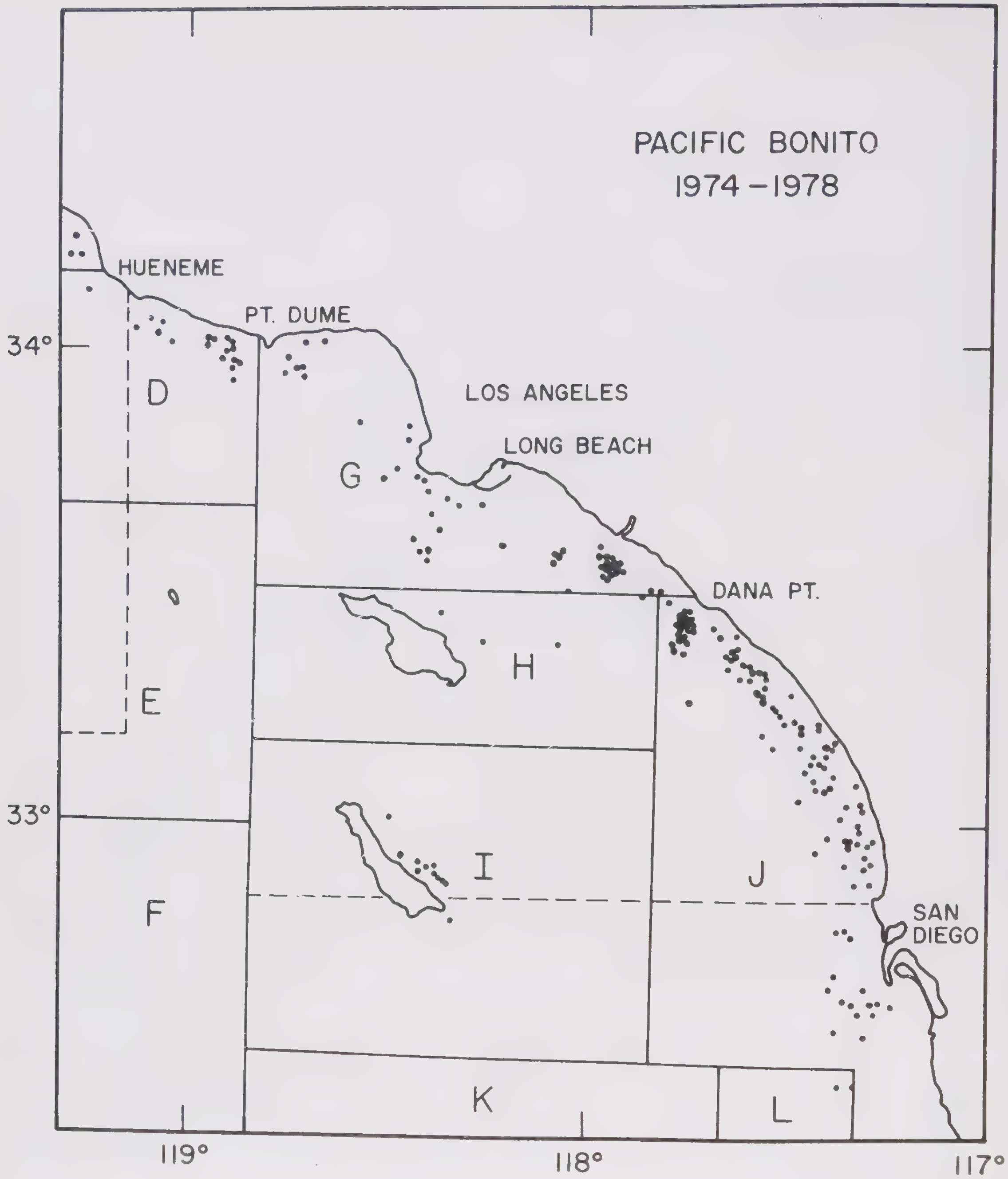

Figure 27.—Pacific bonito—location of centers of sighting for school or school groups, Pt. Hueneme to San Diego, 1974-78.

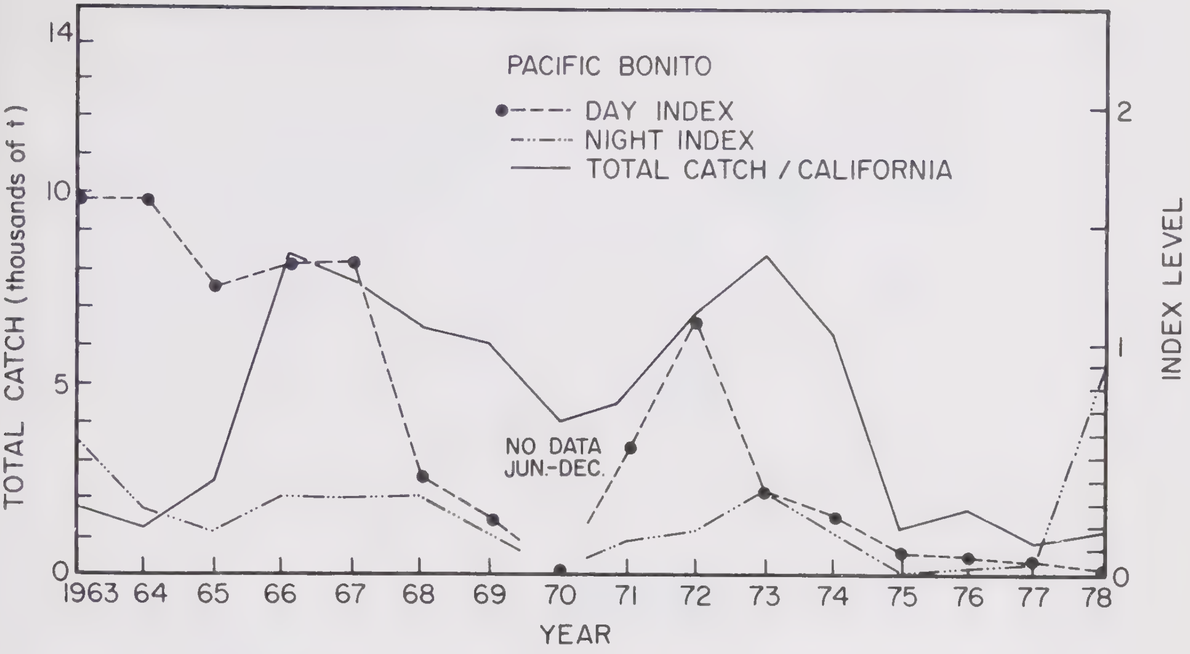

Figure 28.—Pacific bonito index values in arbitrary units for day and night observations and total California catch.

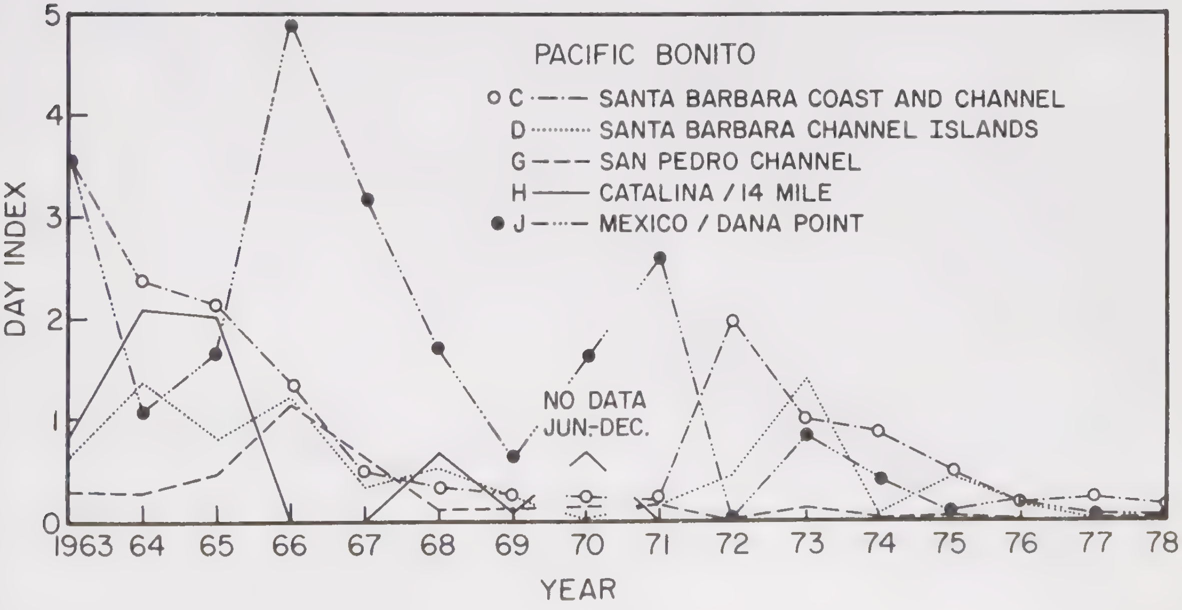

Figure 29.—Pacific bonito day index values in arbitrary units for the major fishing areas.

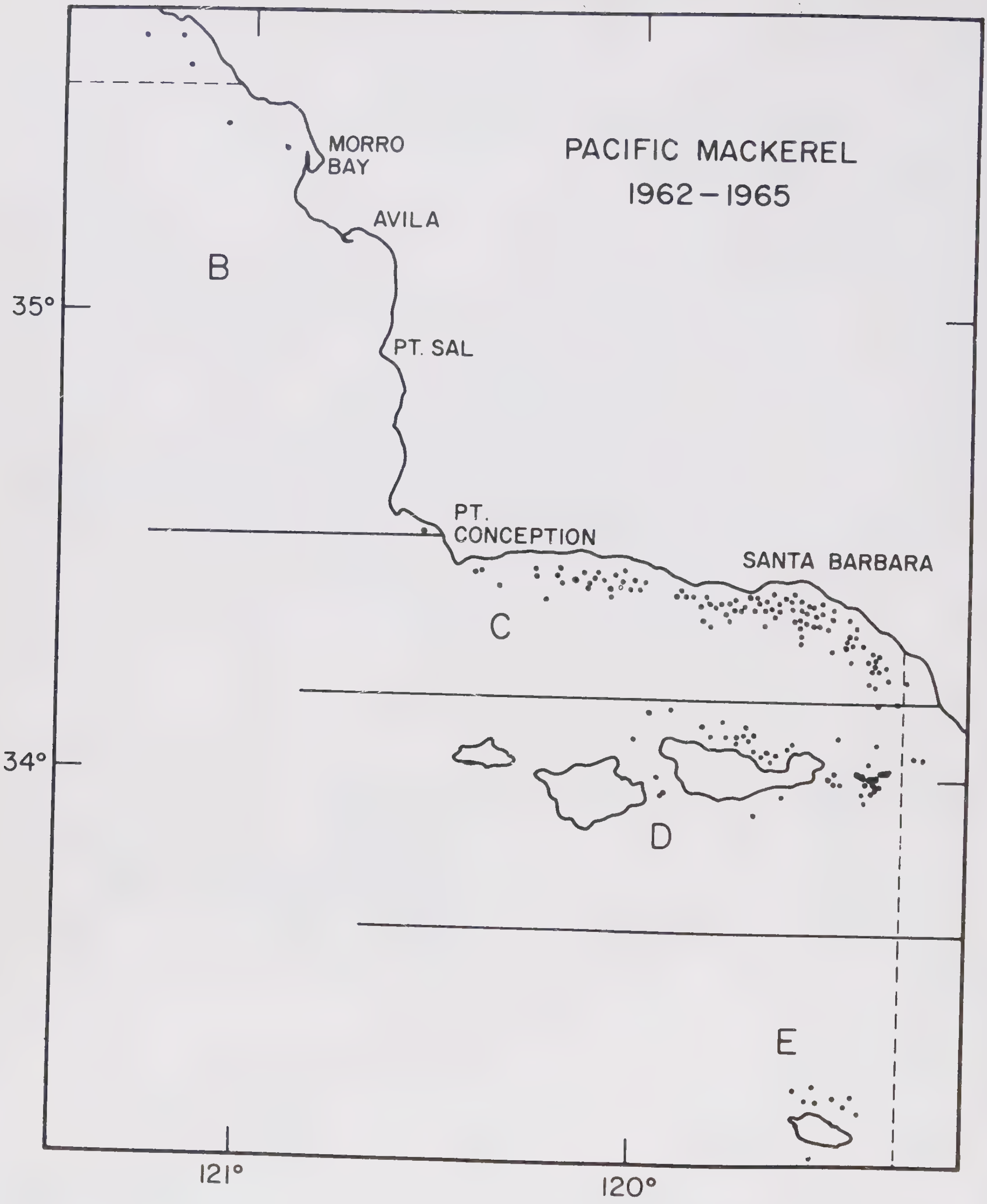

Figure 30.—Pacific mackerel—location of centers of sighting for school or school groups, Morro Bay to San Nicolas Island, 1962-65.

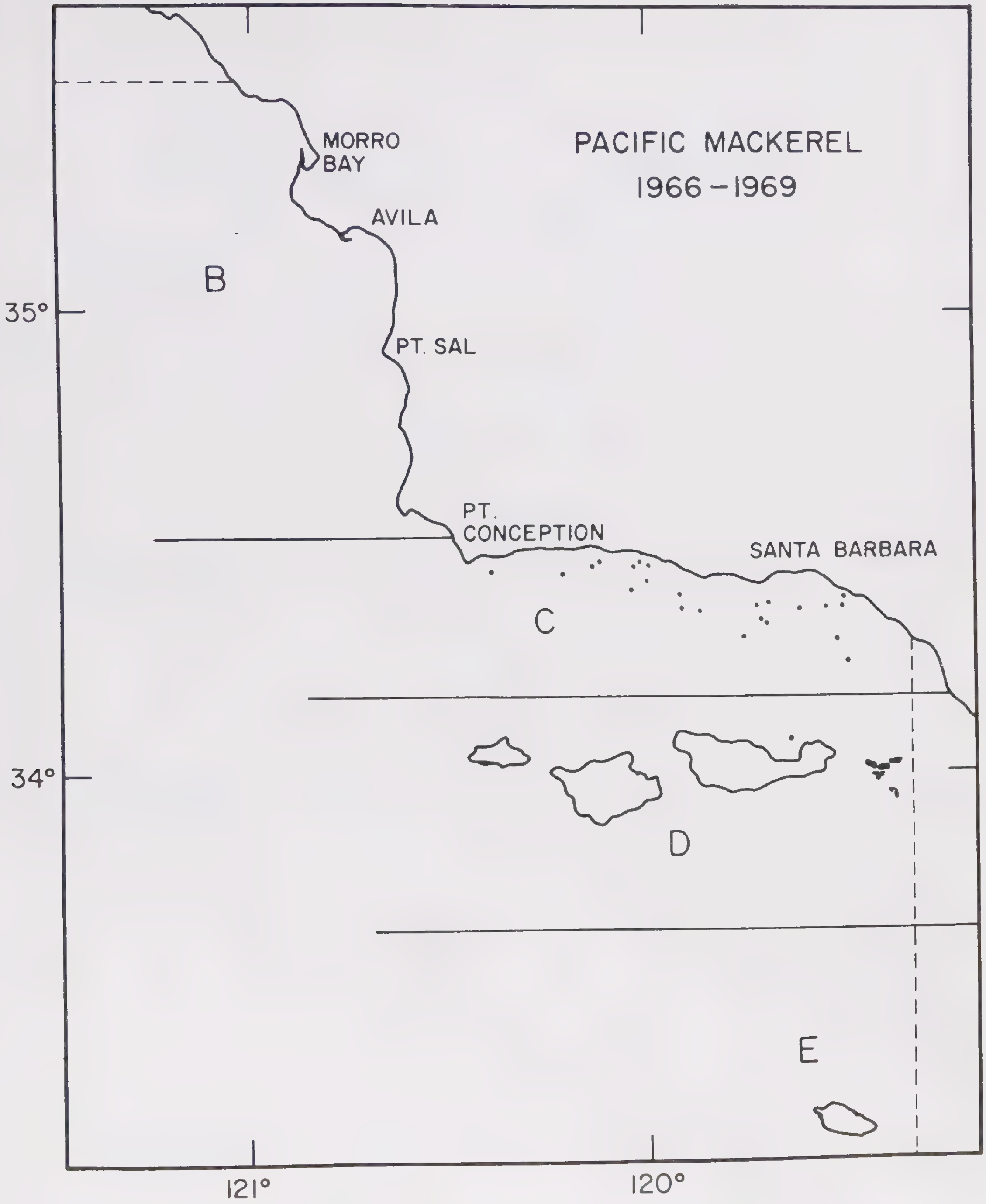

Figure 31.—Pacific mackerel—location of centers of sighting for school or school groups, Morro Bay to San Nicolas Island, 1966-69.

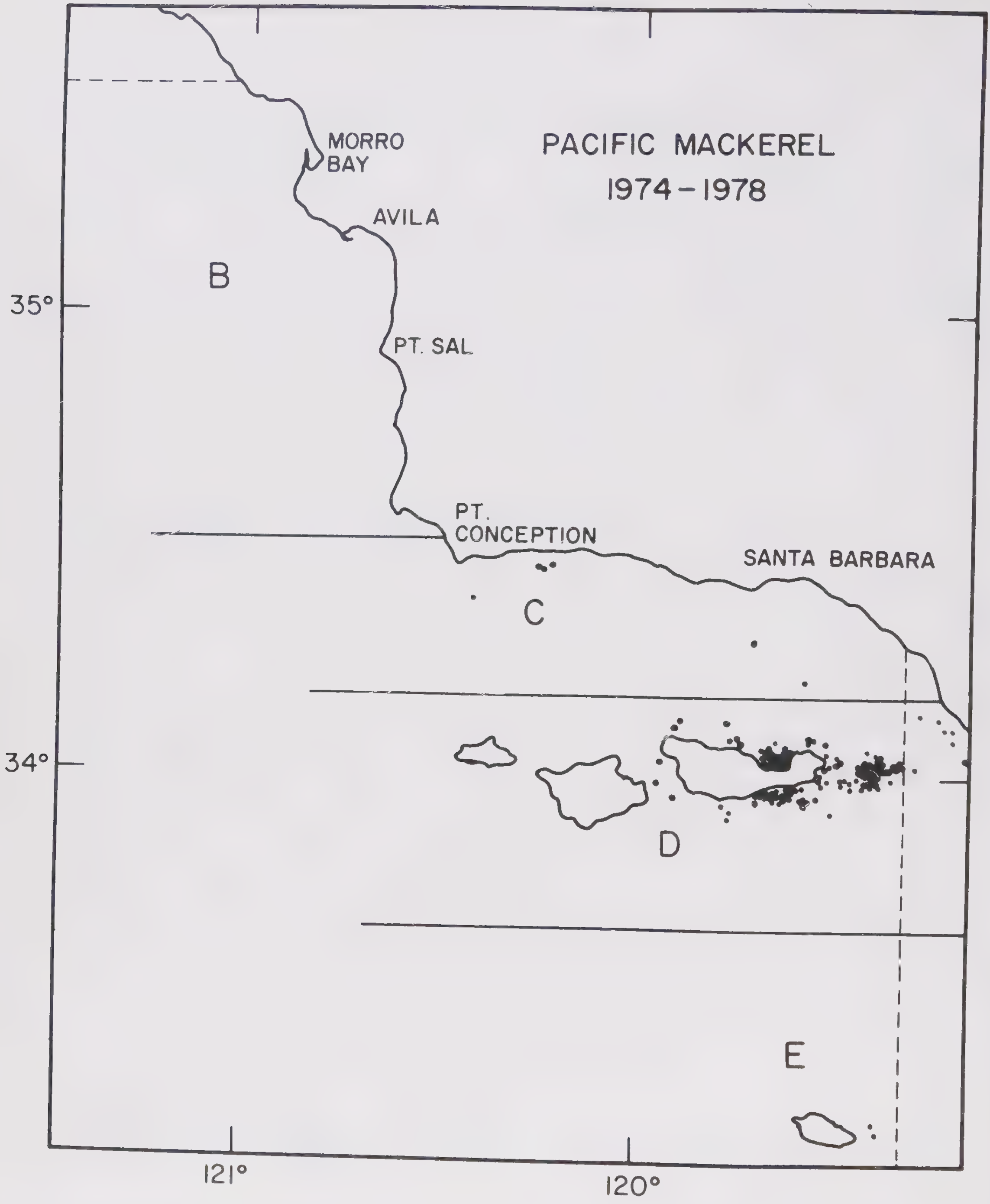

Figure 32.—Pacific mackerel—location of centers of sighting for school or school groups, Morro Bay to San Nicolas Island, 1974-78.

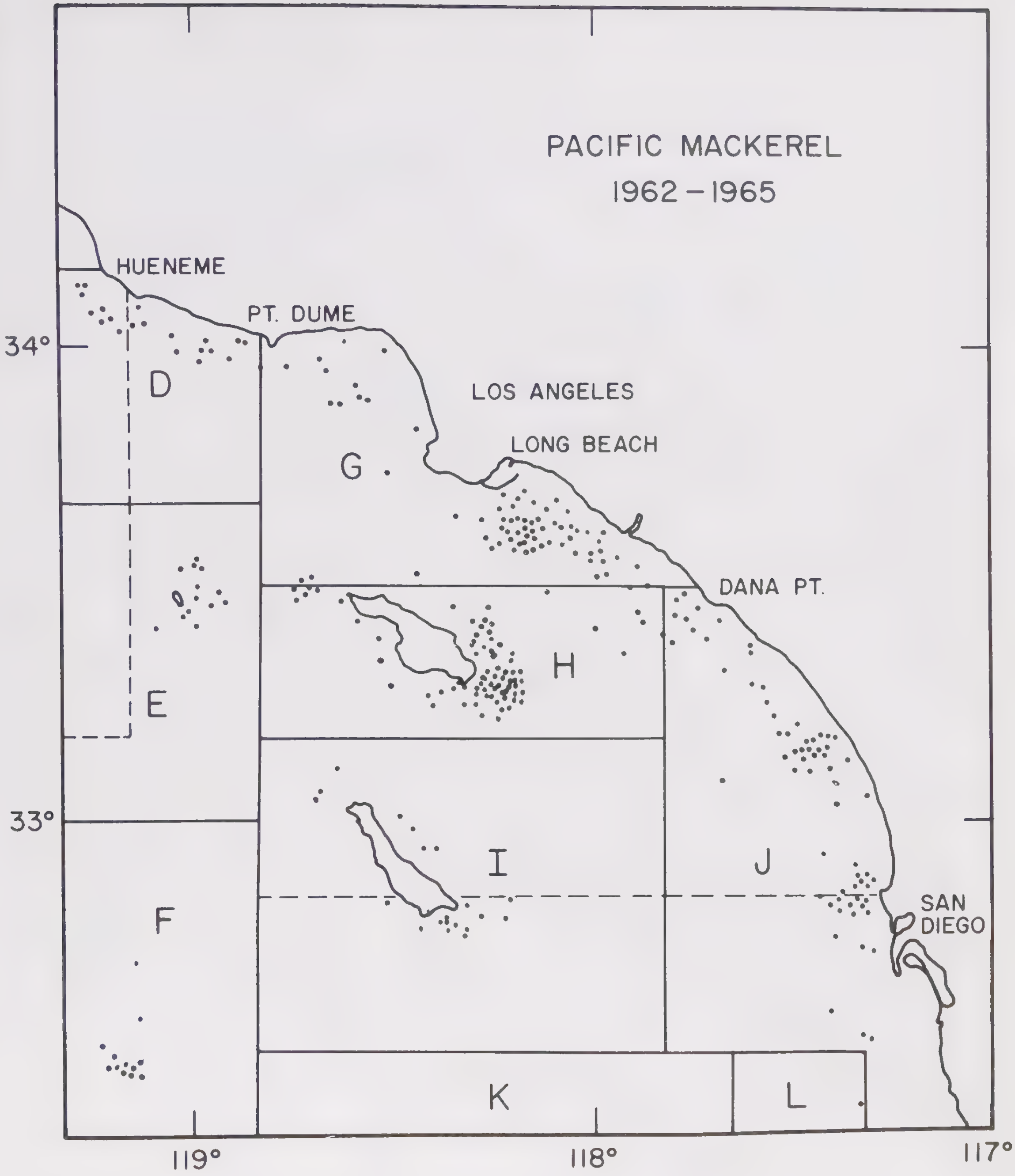

Figure 33.—Pacific mackerel—location of centers of sighting for school or school groups, Pt. Hueneme to San Diego, 1962-65.

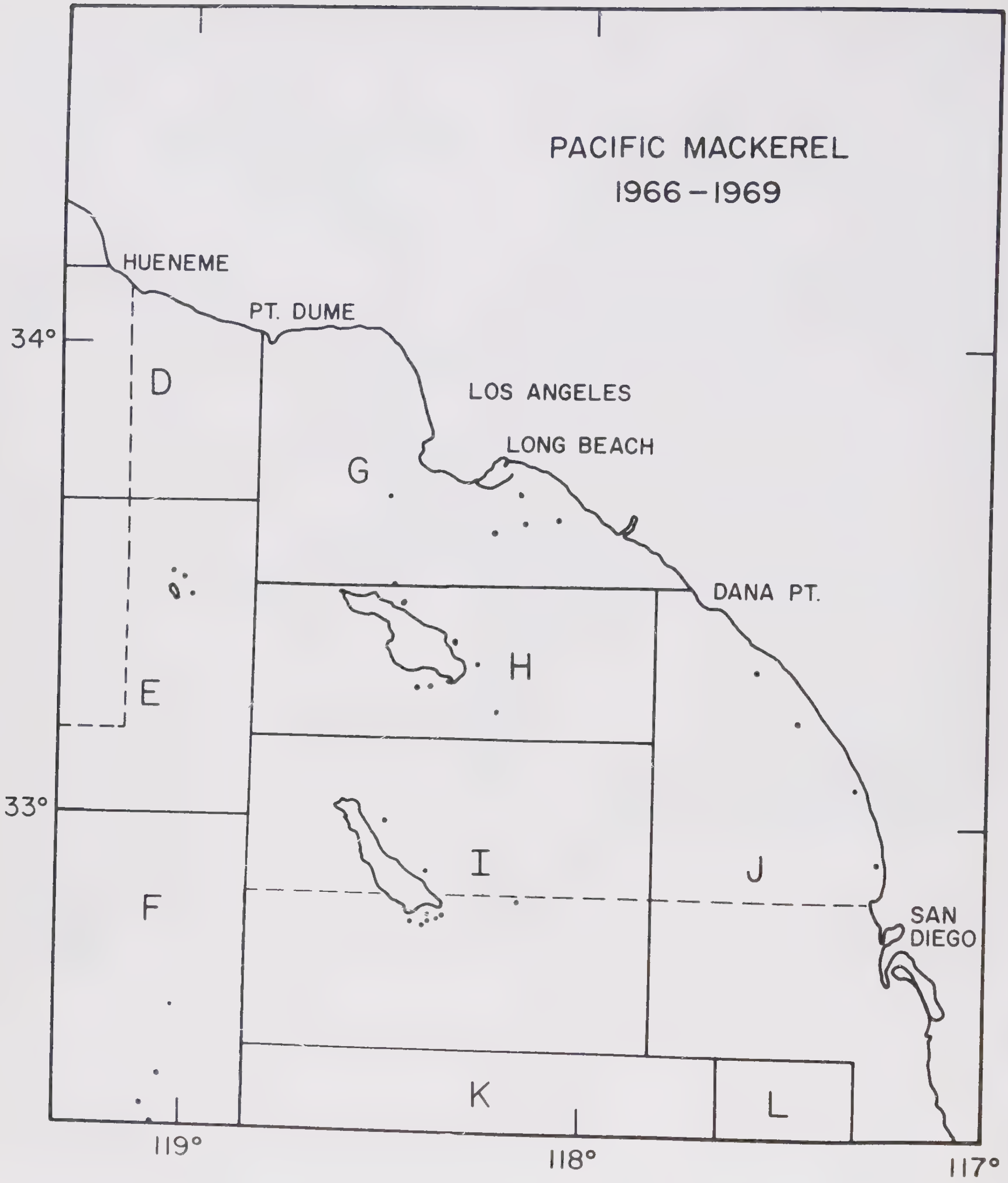

Figure 34.—Pacific mackerel—location of centers of sighting for school or school groups, Pt. Hueneme to San Diego, 1966-69.

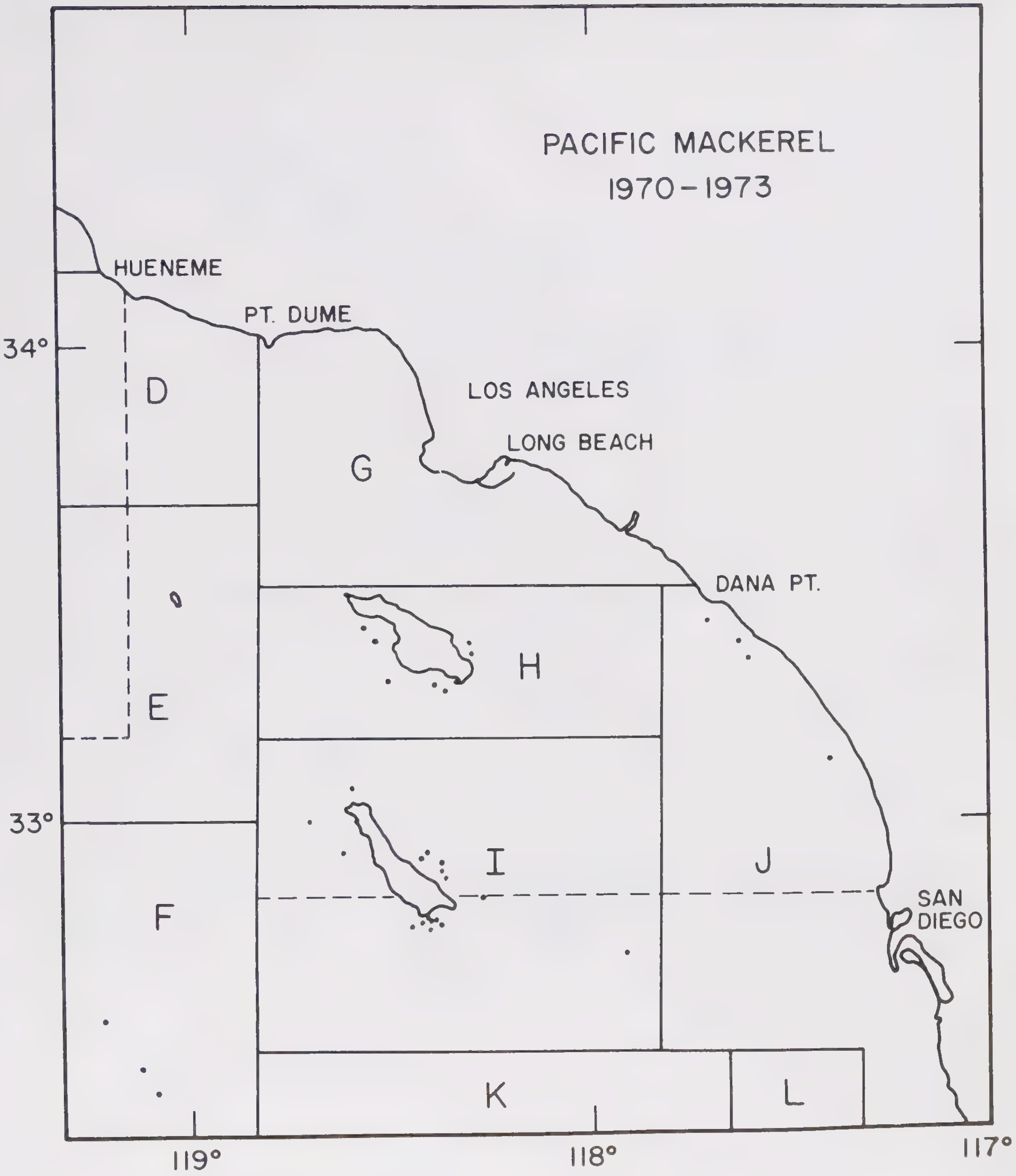

Figure 35.—Pacific mackerel—location of centers of sighting for school or school groups, Pt. Hueneme to San Diego, 1970-73.

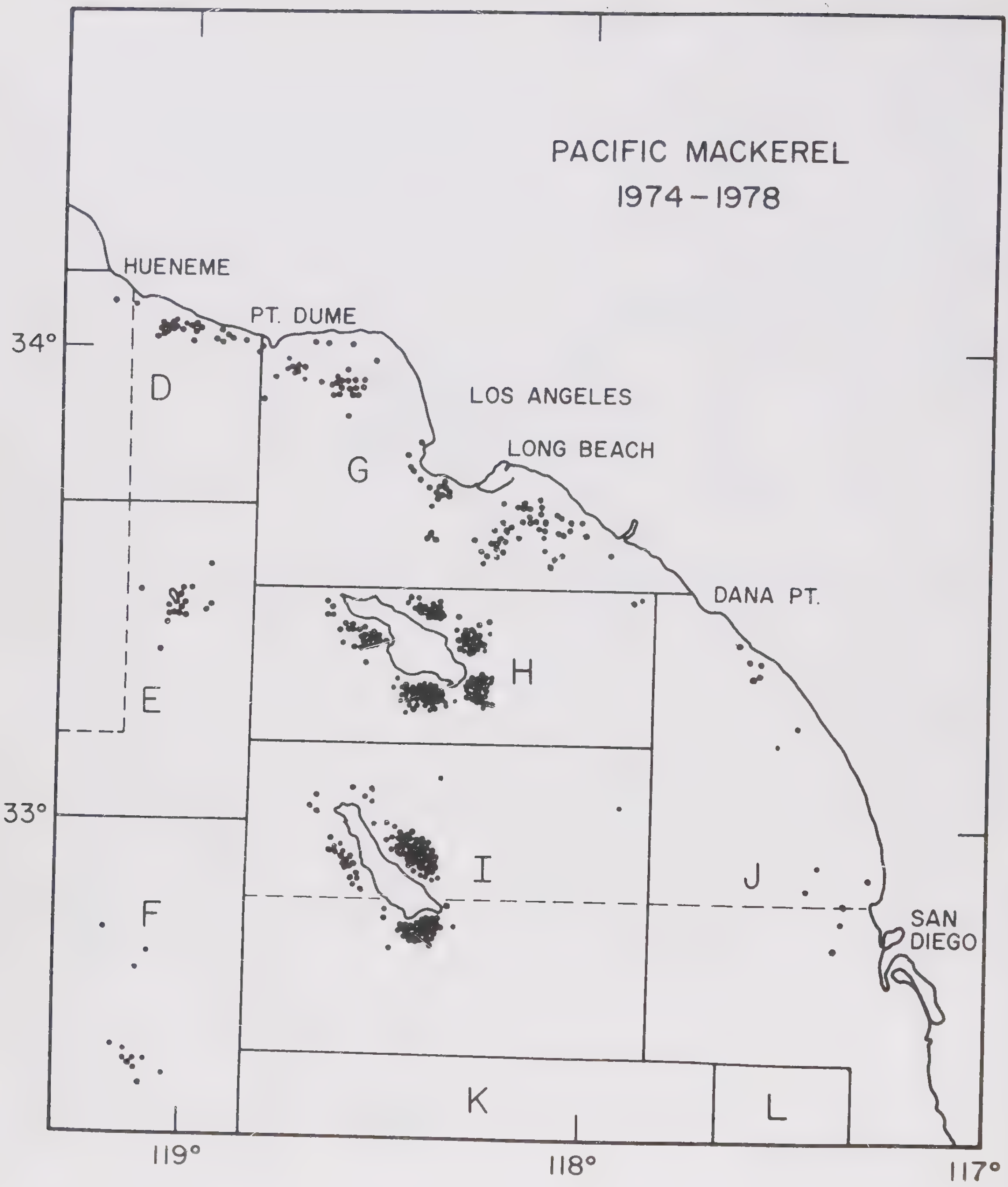

Figure 36.—Pacific mackerel—location of centers of sighting for school or school groups, Pt. Hueneme to San Diego, 1974-78.

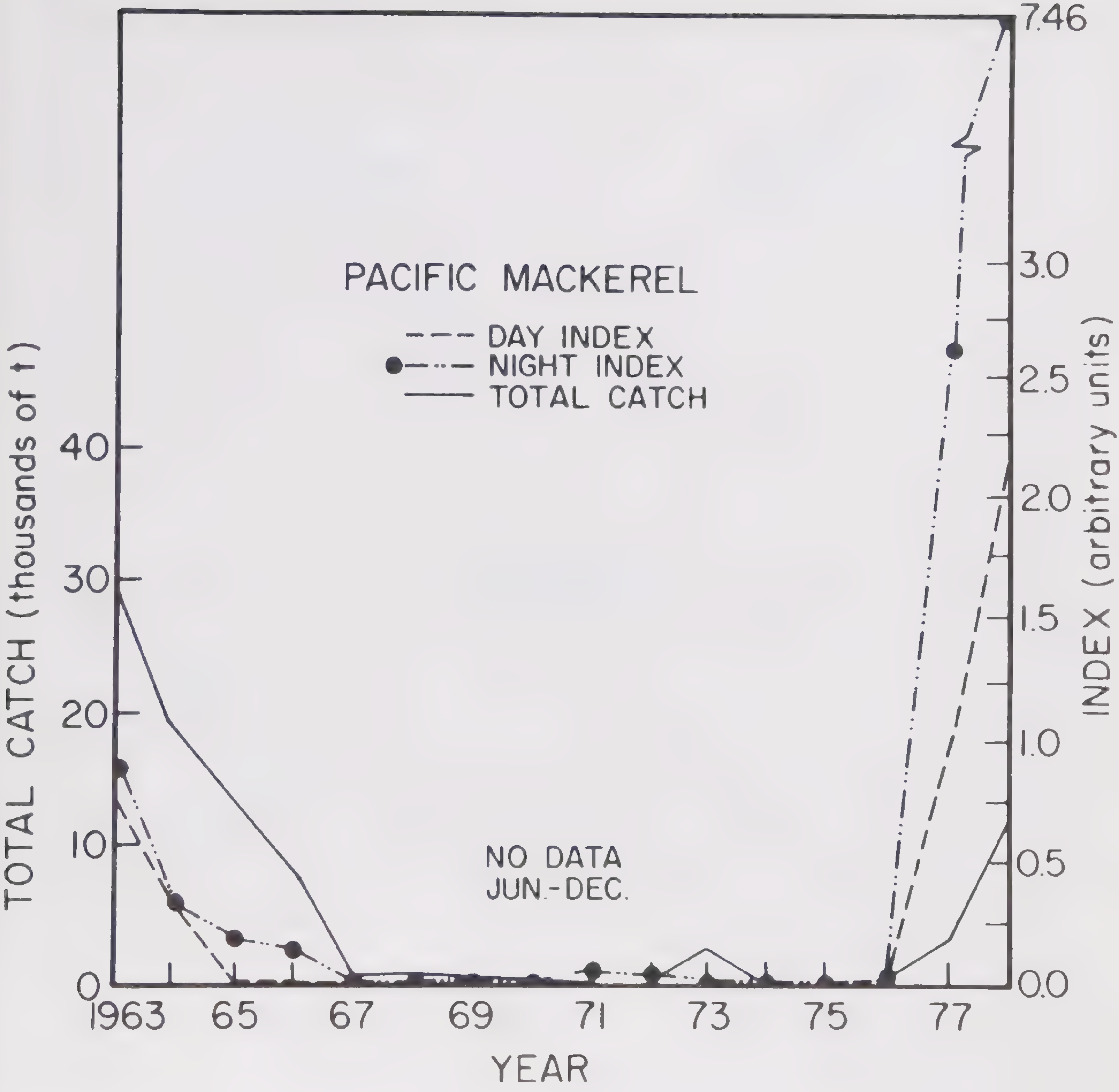

Figure 37. - Pacific mackerel index values in arbitrary units for day and night observations and total California catch.

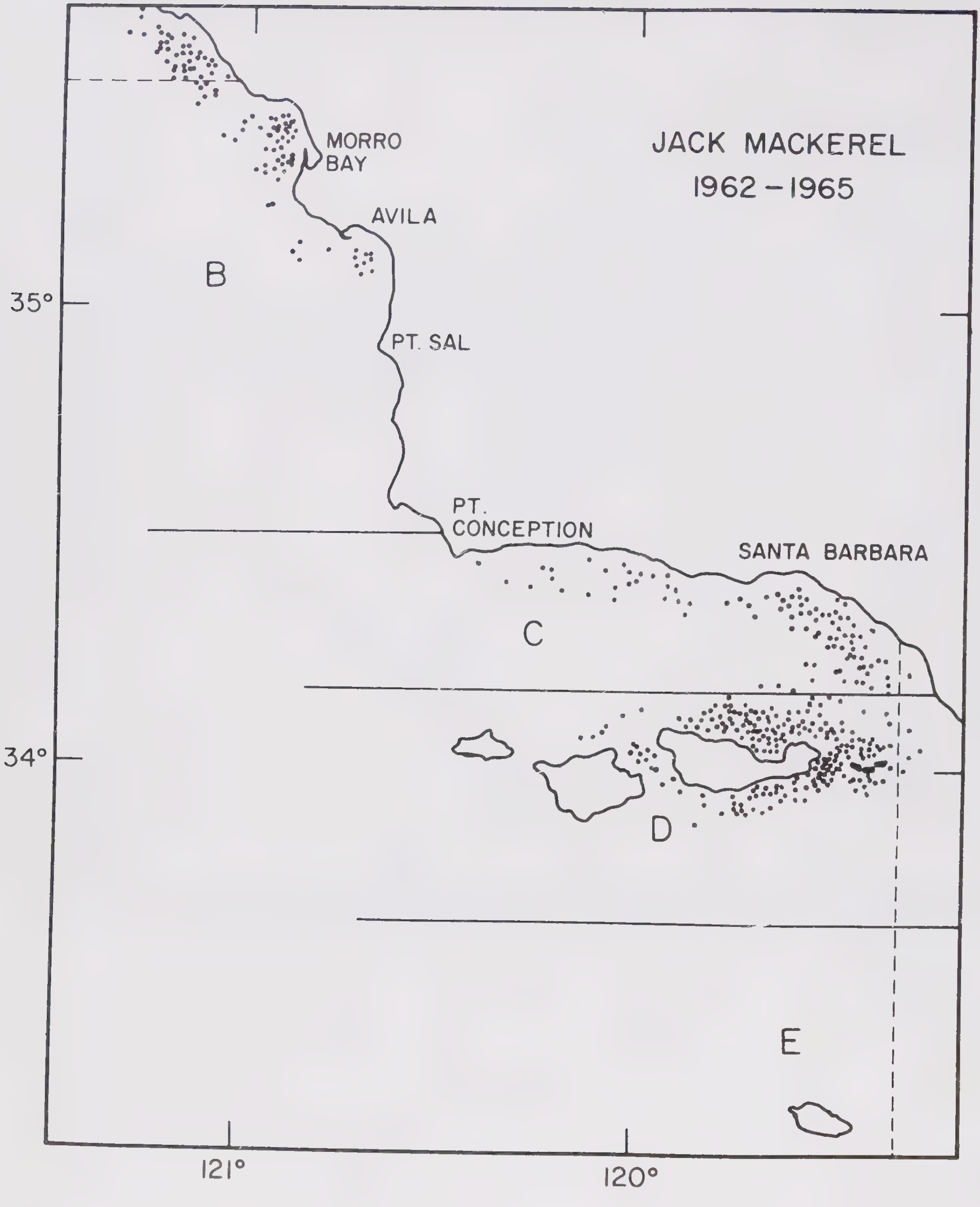

Figure 38.—Jack mackerel—location of centers of sighting for school or school groups, Morro Bay to San Nicolas Island, 1962-65.

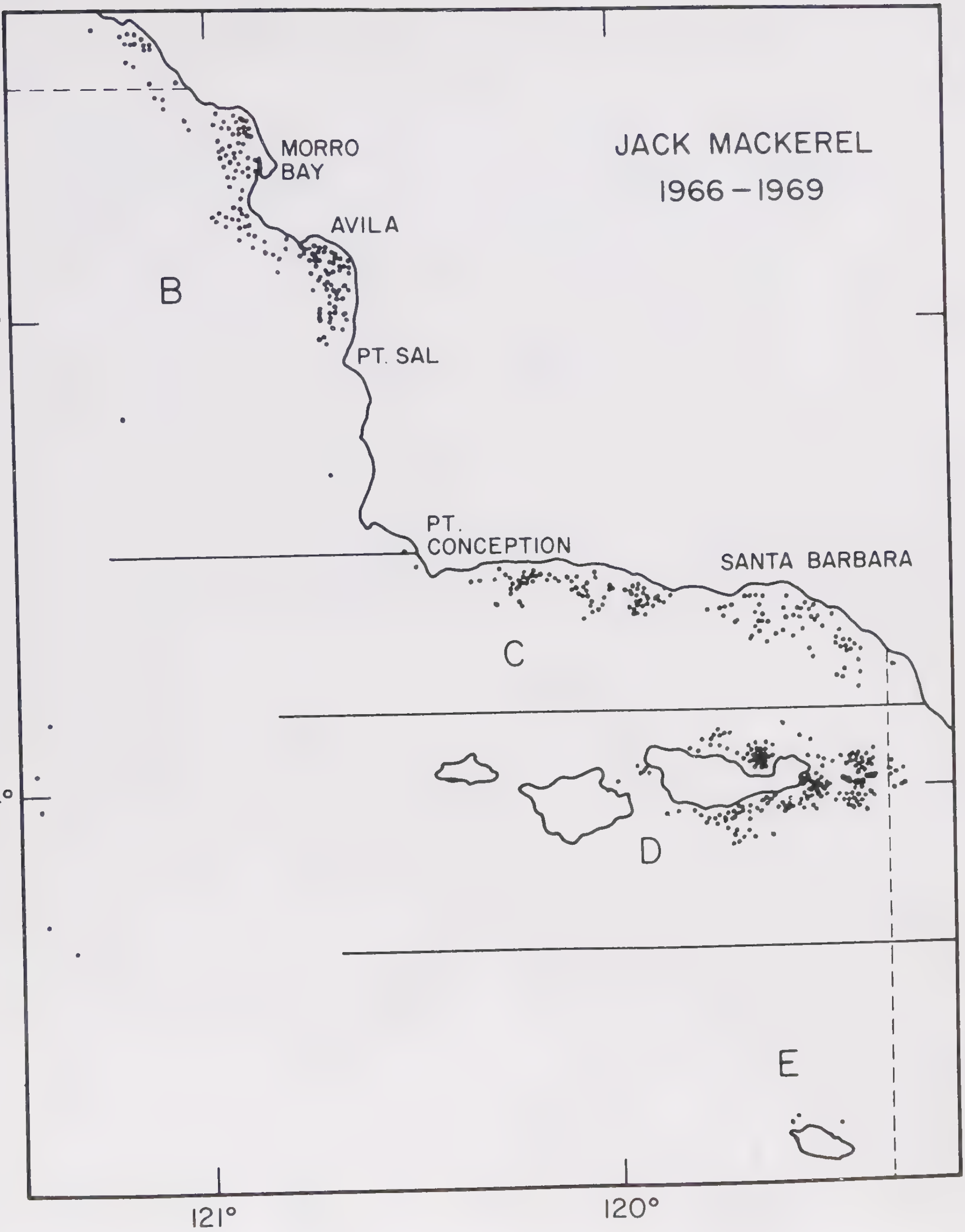

Figure 39.—Jack mackerel—location of centers of sighting for school or school groups, Morro Bay to San Nicolas Island, 1966-69.

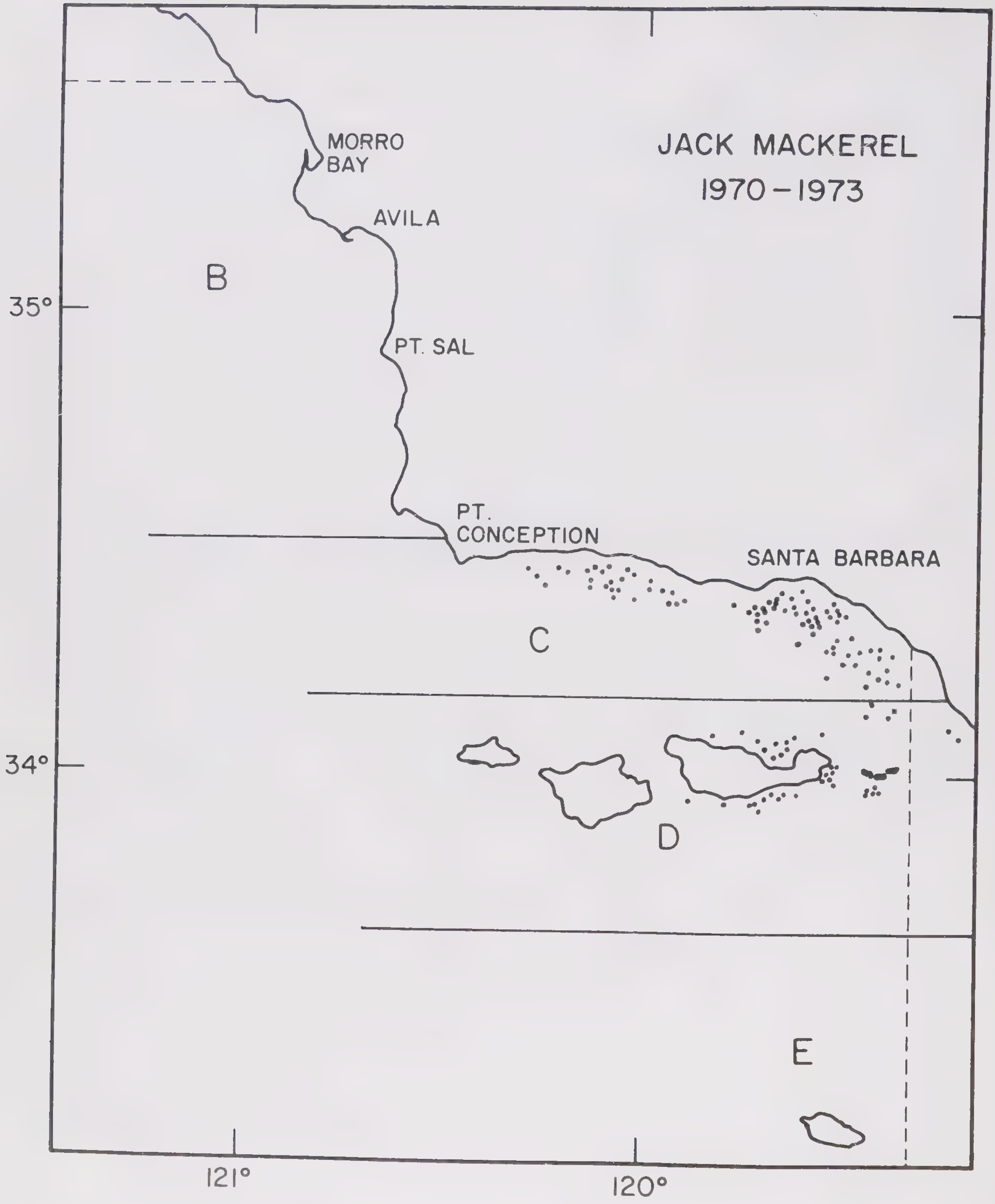

Figure 40.—Jack mackerel—location of centers of sighting for school or school groups, Morro Bay to San Nicolas Island, 1970-73.

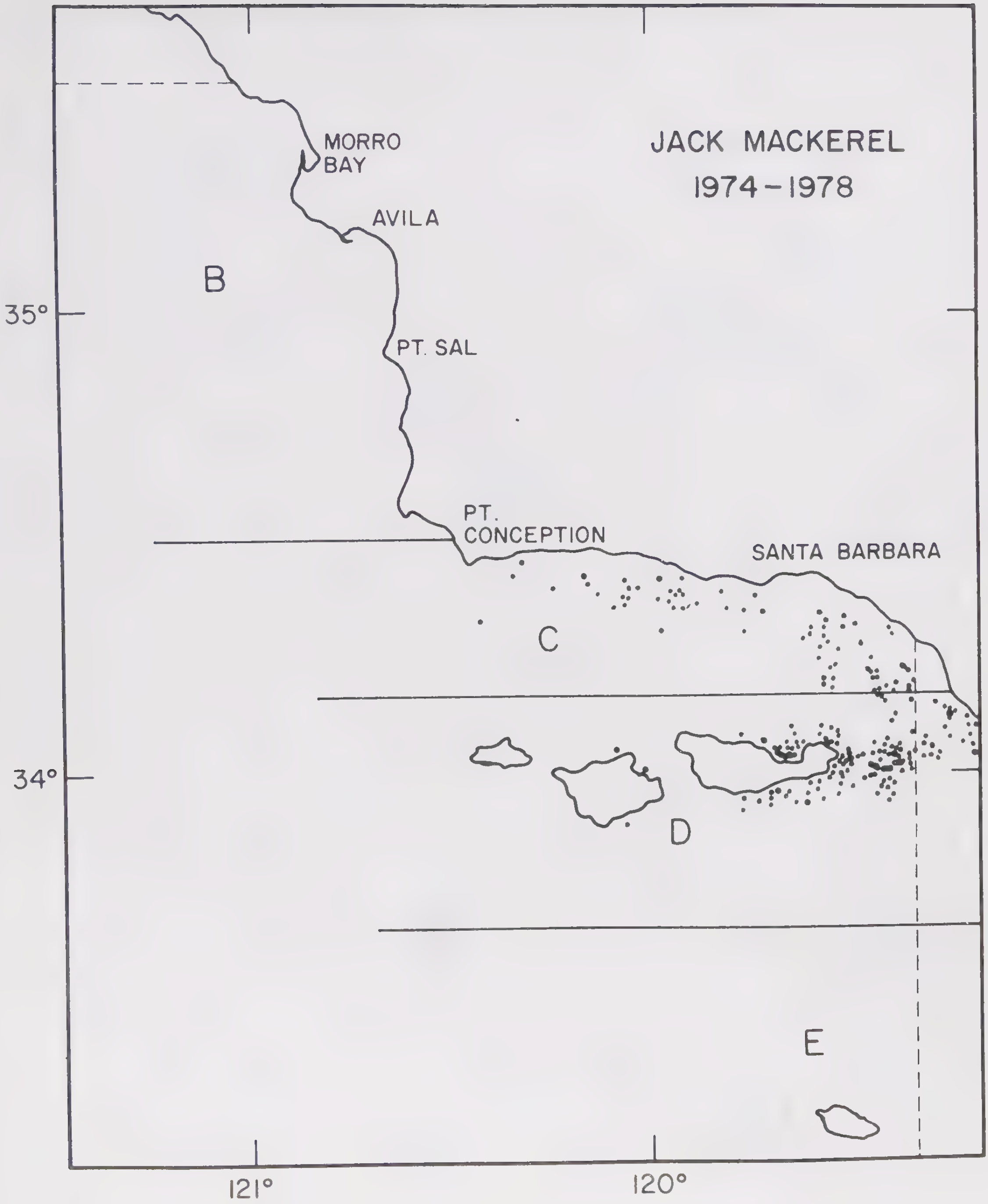

Figure 41.—Jack mackerel—location of centers of sighting for school or school groups, Morro Bay to San Nicolas Island, 1974-78.

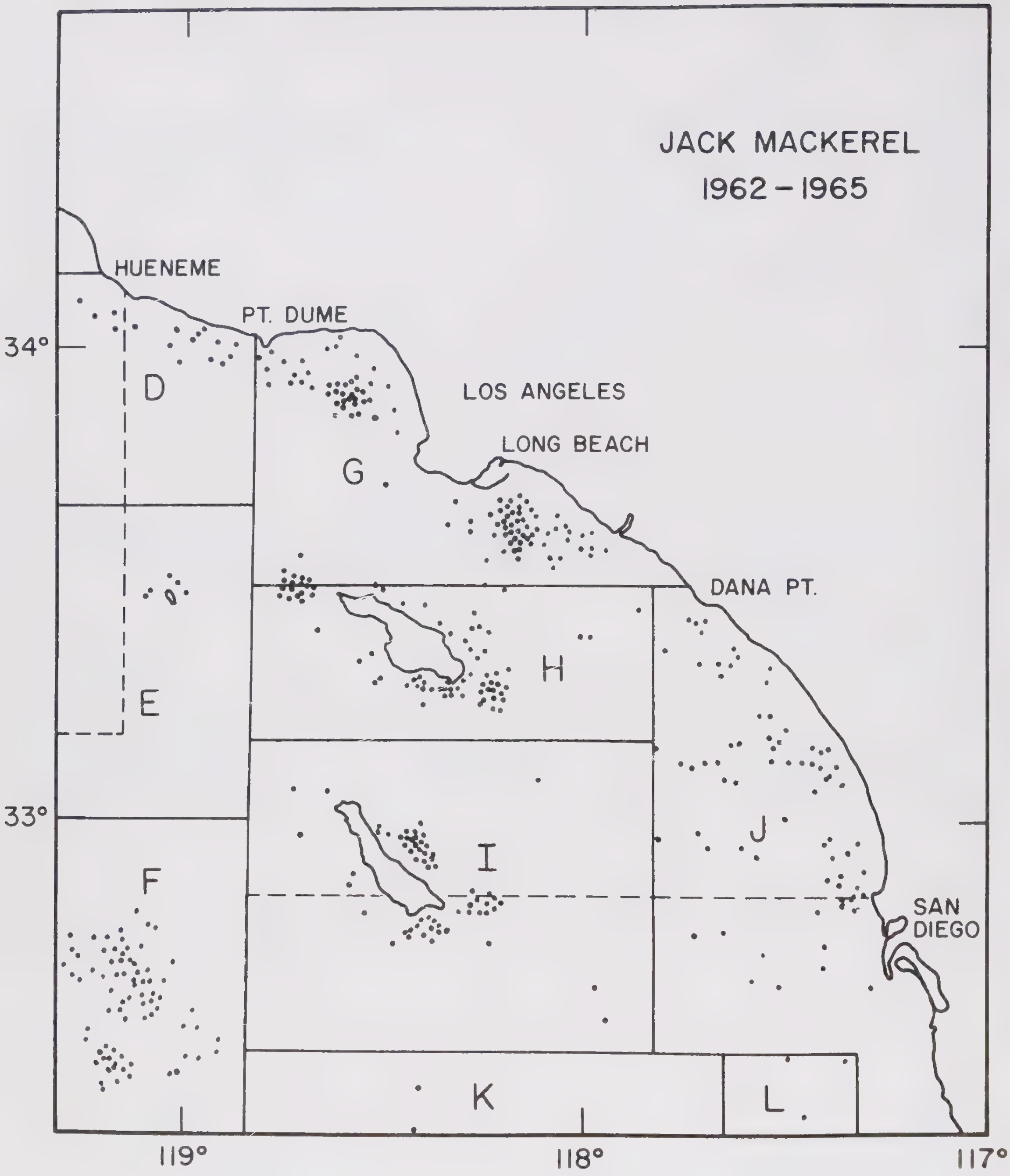

Figure 42.—Jack mackerel—location of centers of sighting for school or school groups, Pt. Hueneme to San Diego, 1962-65.

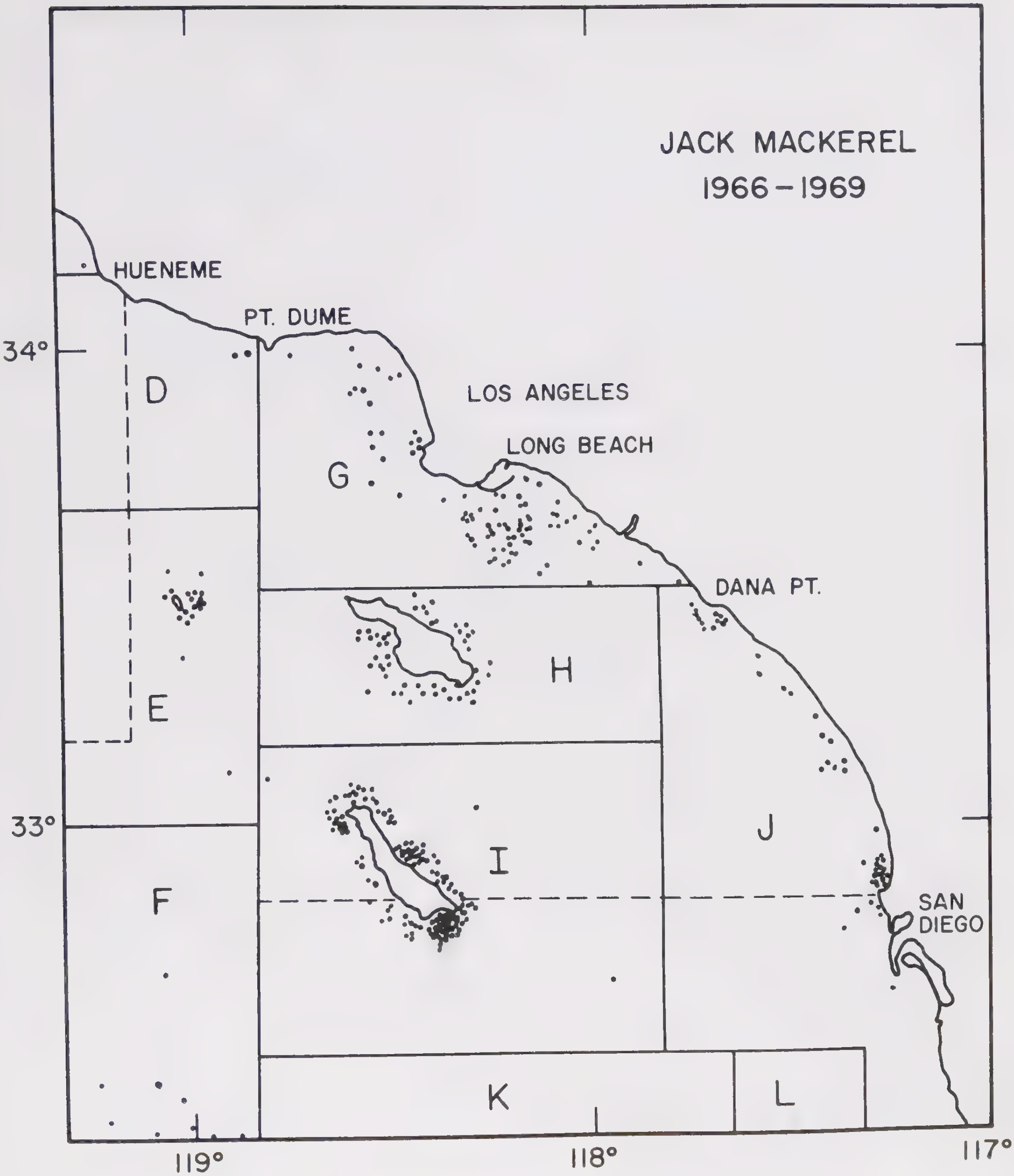

Figure 43.—Jack mackerel—location of centers of sighting for school or school groups, Pt. Hueneme to San Diego, 1966-69.

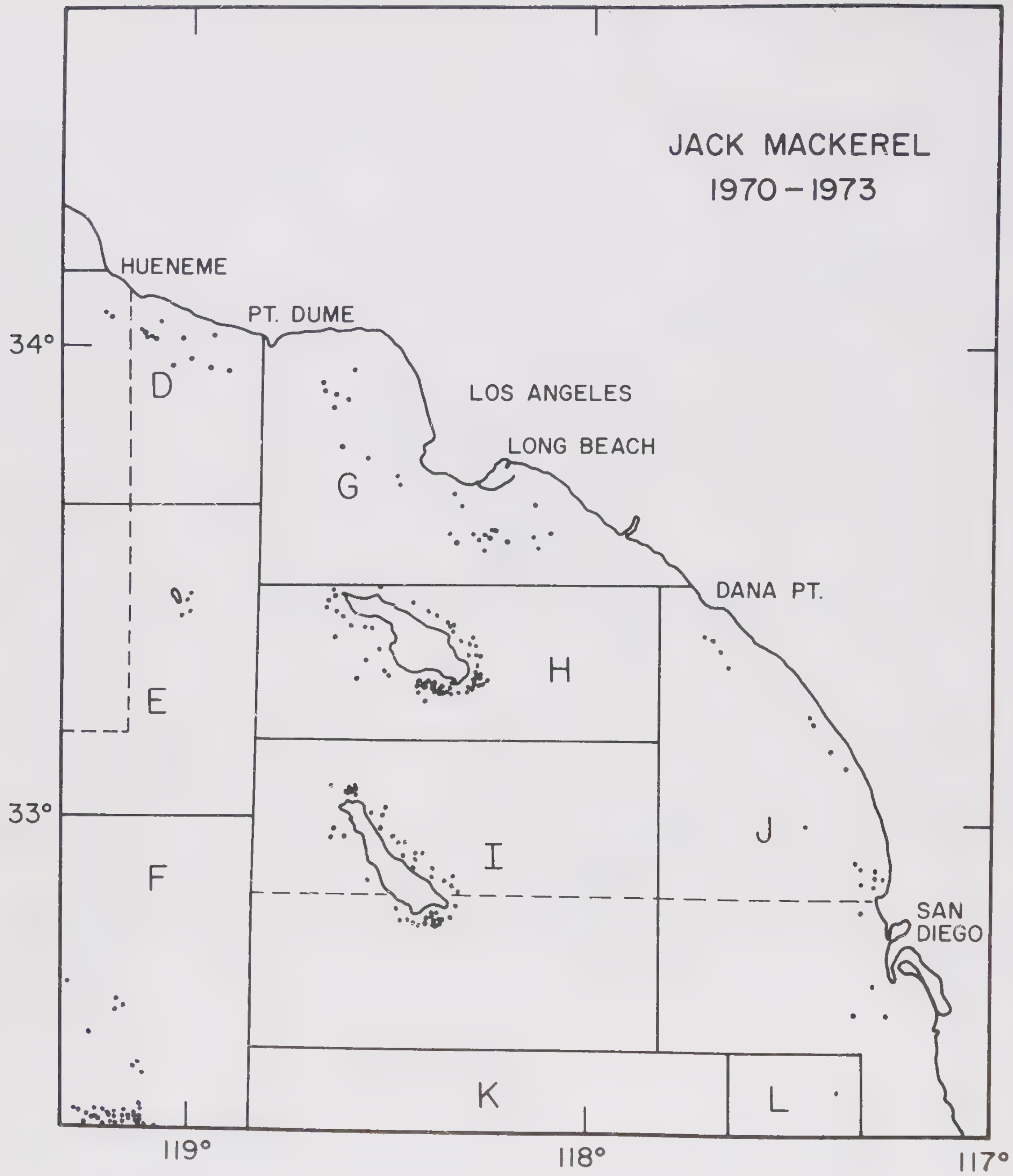

Figure 44.—Jack mackerel—location of centers of sighting for school or school groups, Pt. Hueneme to San Diego, 1970-73.

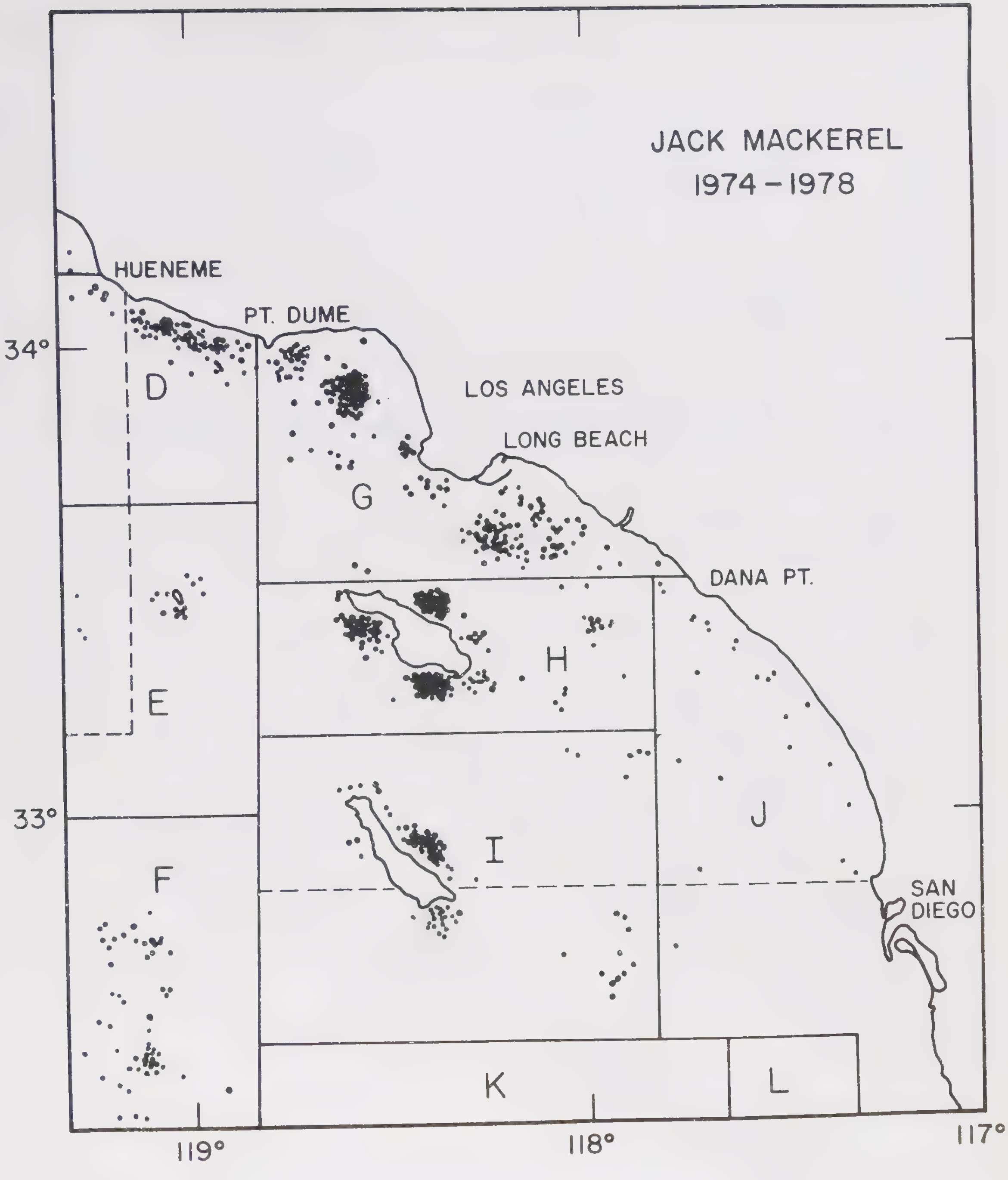

Figure 45.—Jack mackerel—location of centers of sighting for school or school groups, Pt. Hueneme to San Diego, 1974-78.

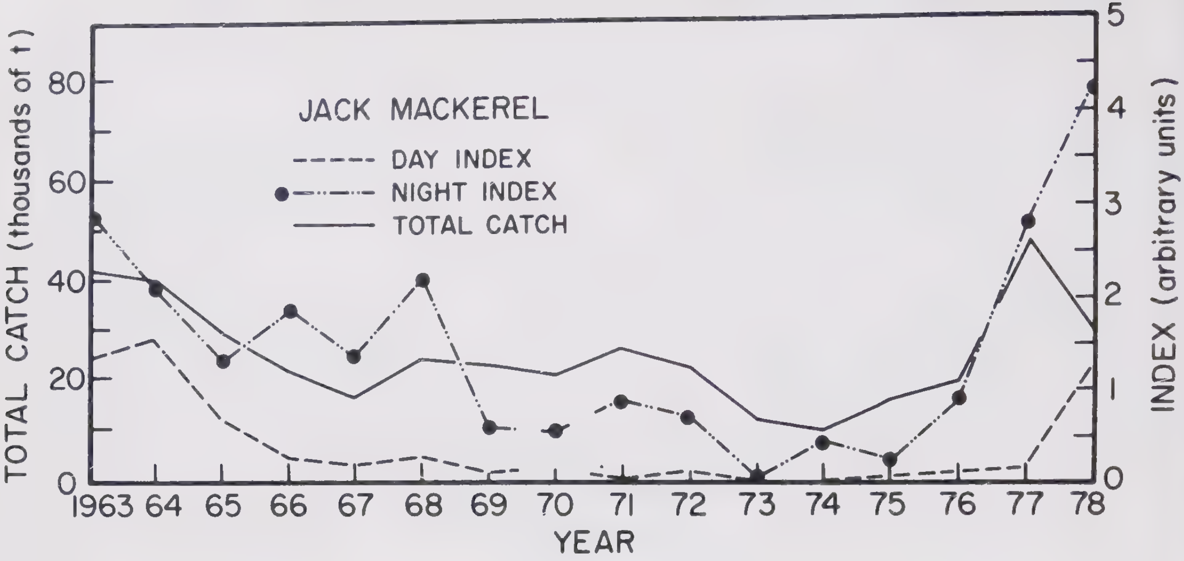

Figure 46.—Jack mackerel index values in arbitrary units for day and night observations and total California catch.

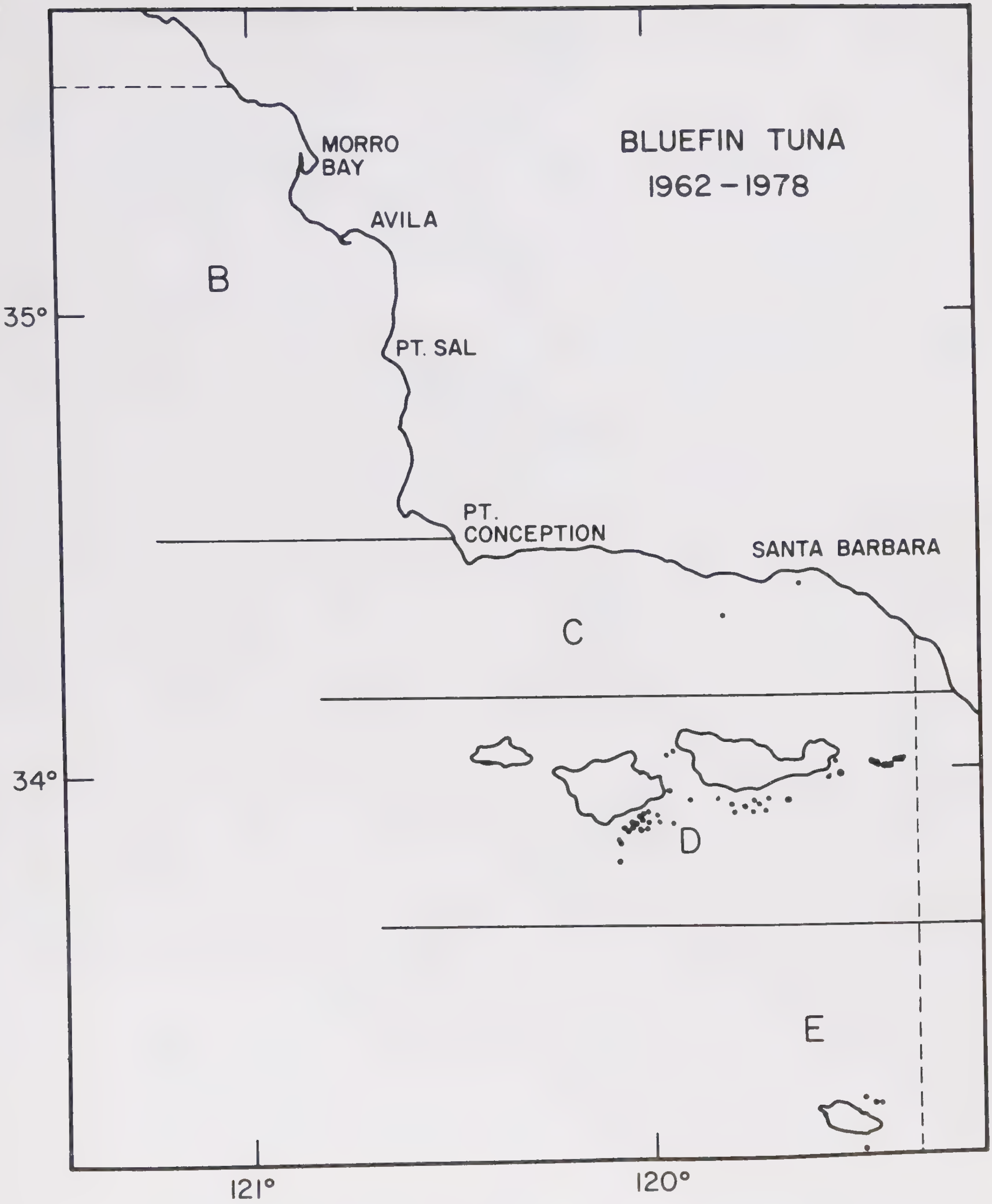

Figure 47.—Bluefin tuna—location of centers of sighting for school or school groups, Morro Bay to San Nicolas Island, 1962-78.

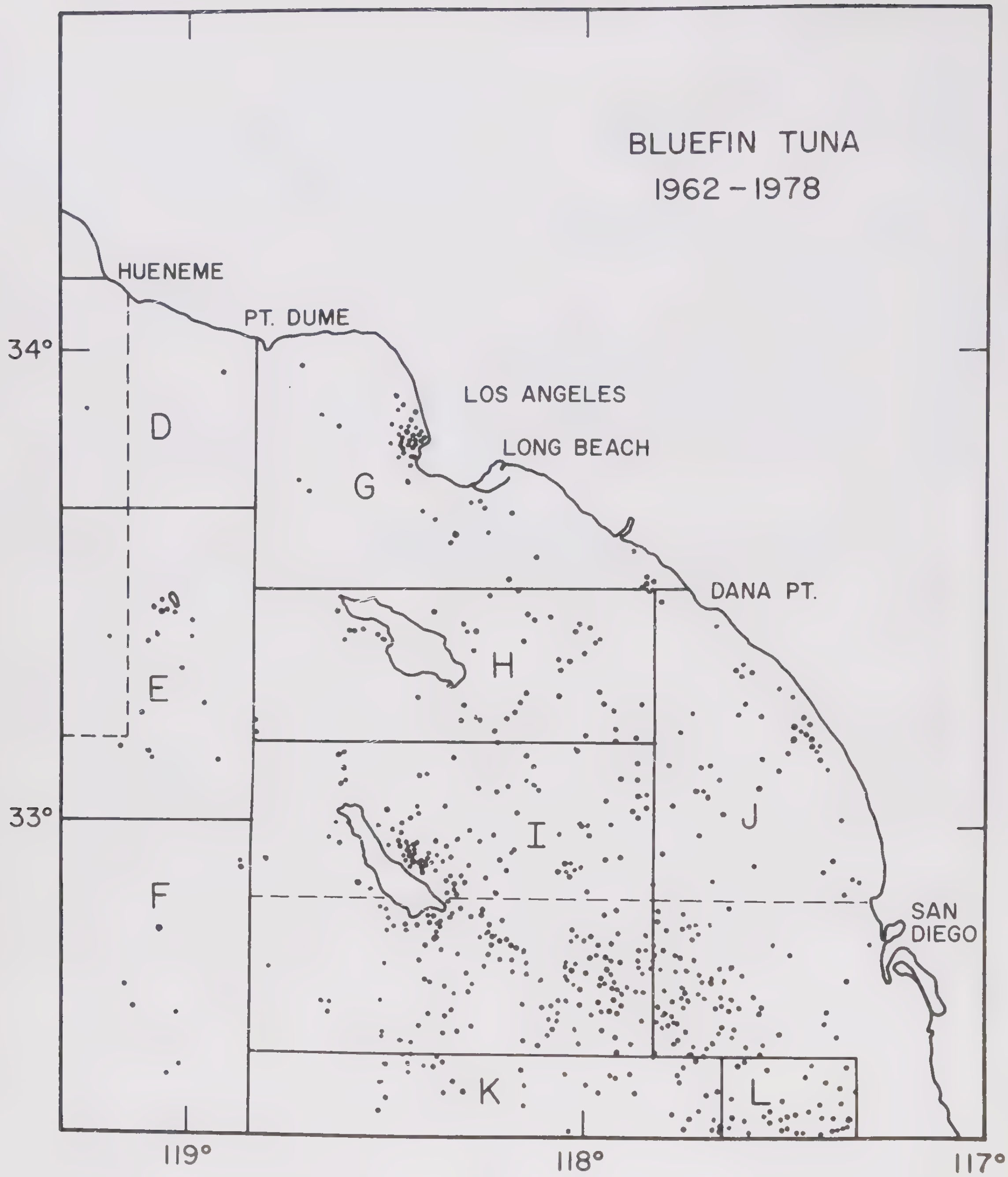

Figure 48.—Bluefin tuna—location of centers of sighting for school or school groups, Pt. Hueneme to San Diego, 1962-78.

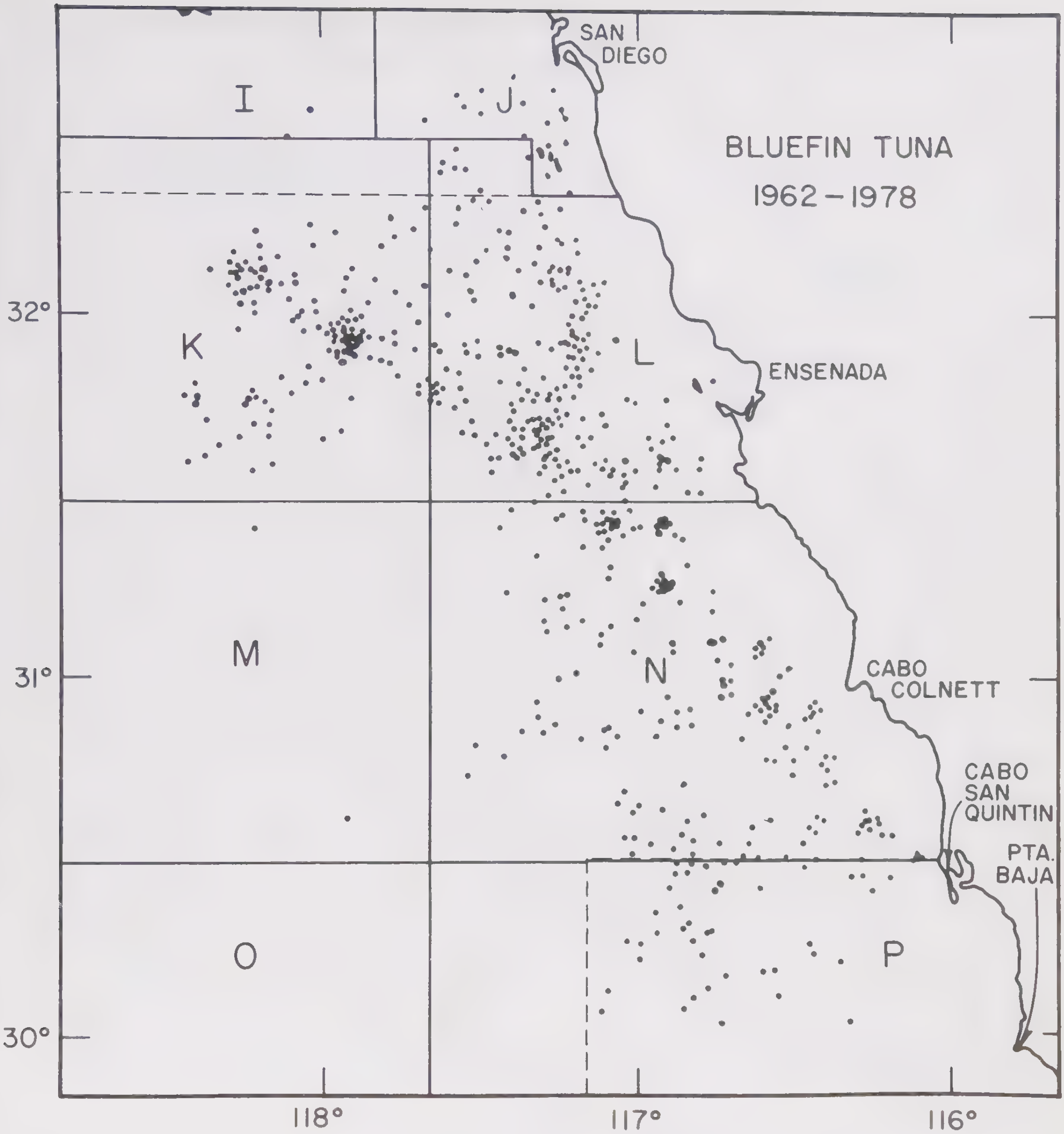

Figure 49.—Bluefin tuna—location of centers of sighting for school or school groups, San Diego to Punta Baja, 1962-78.

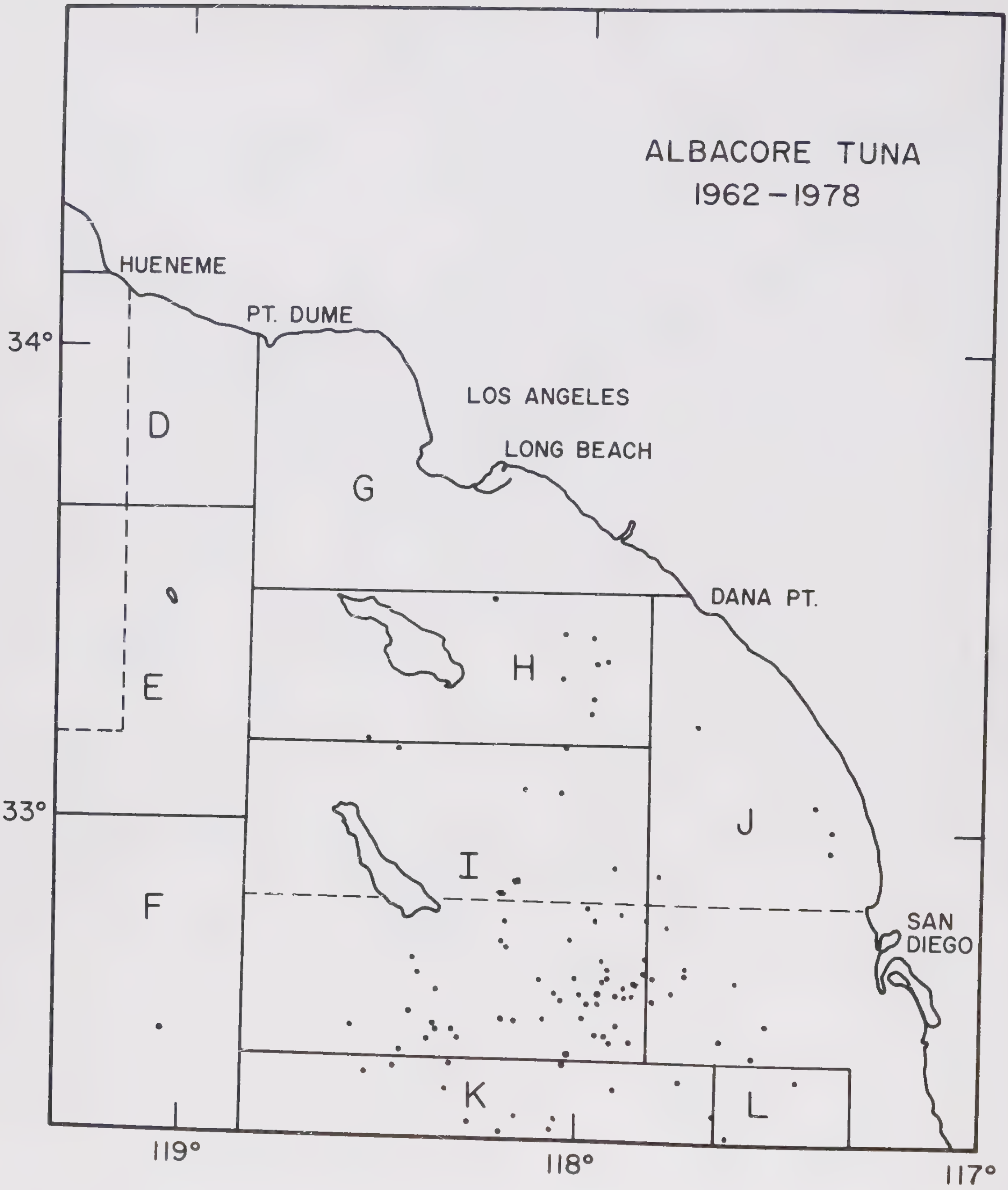

Figure 50.—Albacore tuna—location of centers of sighting for school or school groups, Pt. Hueneme to San Diego, 1962-78.

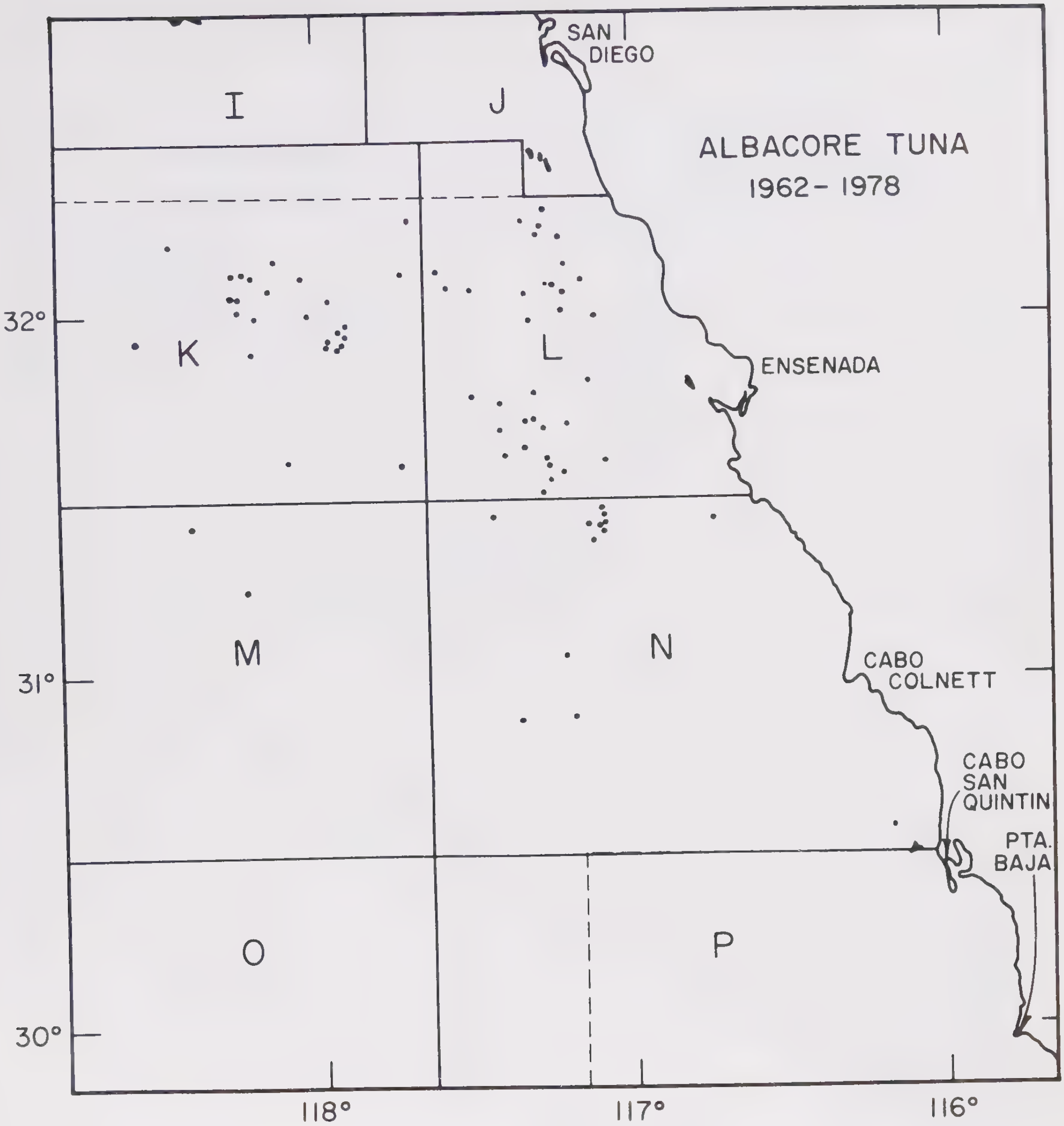

Figure 51.—Albacore tuna—location of centers of sighting for school or school groups, San Diego to Punta Baja, 1962-78.

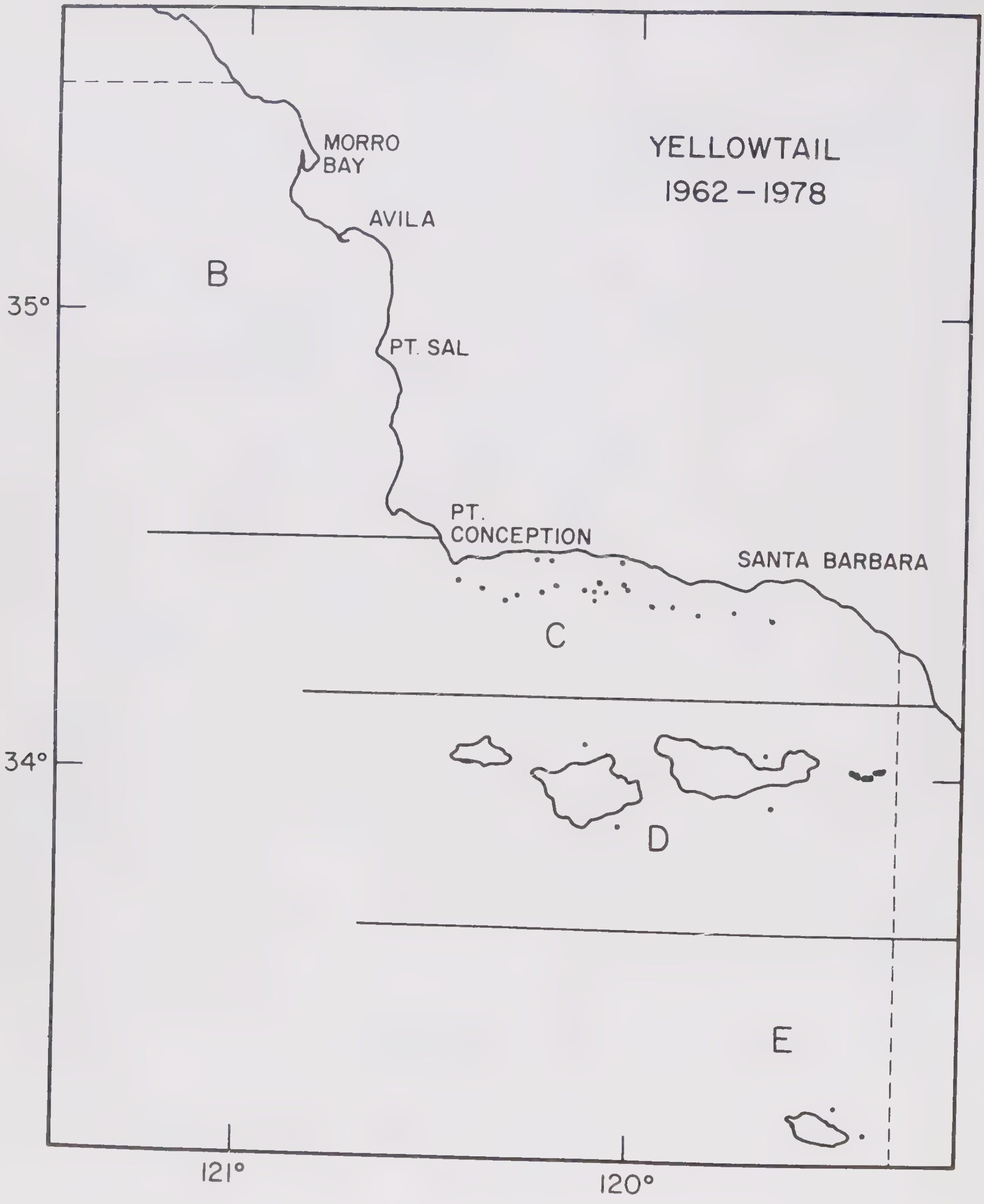

Figure 52.—Yellowtail—locations of school or school group sightings, Morro Bay to San Nicolas Island, 1962-78.

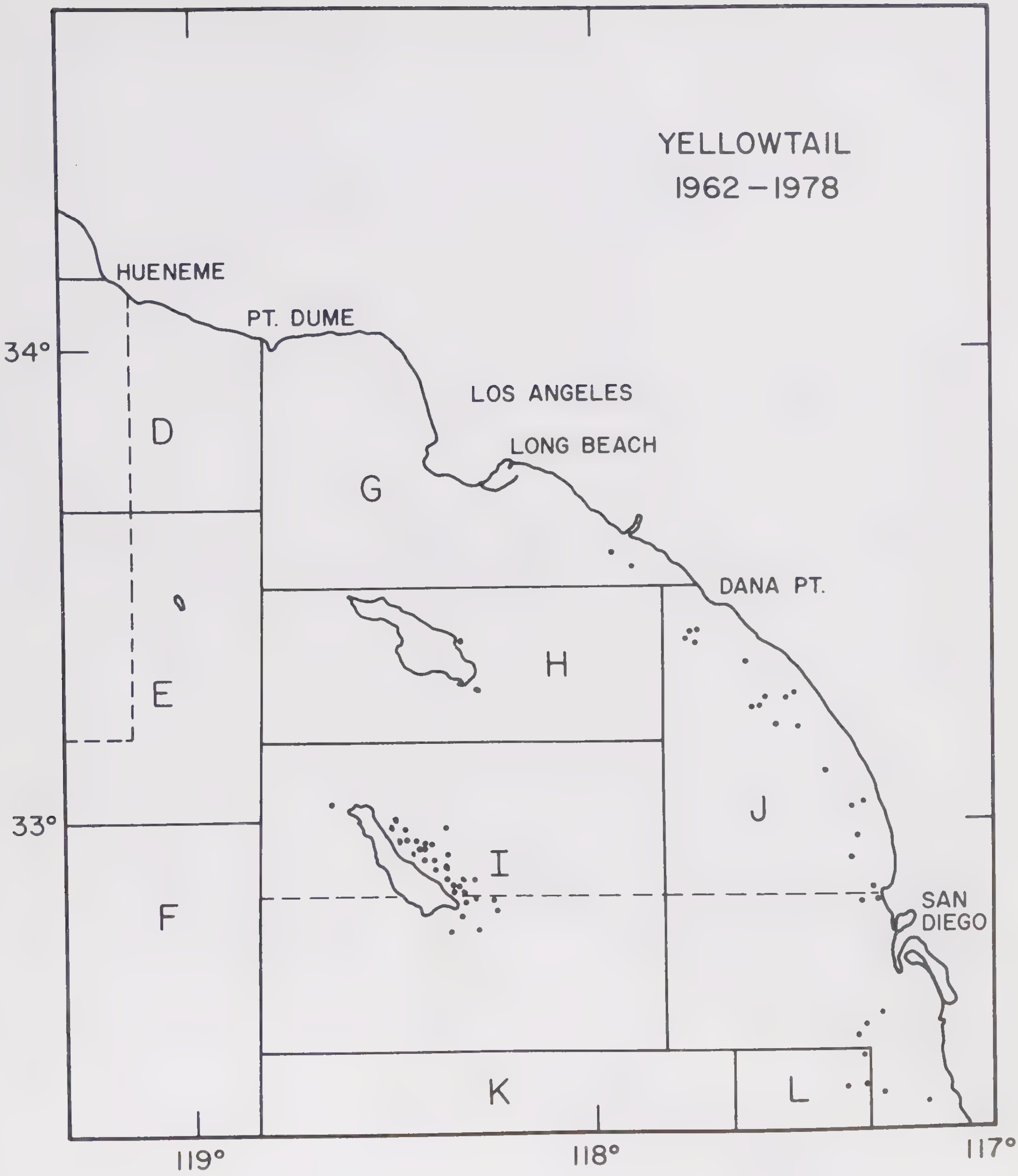

Figure 53.—Yellowtail—location of centers of sighting for school or school groups, Pt. Hueneme to San Diego, 1962-78.

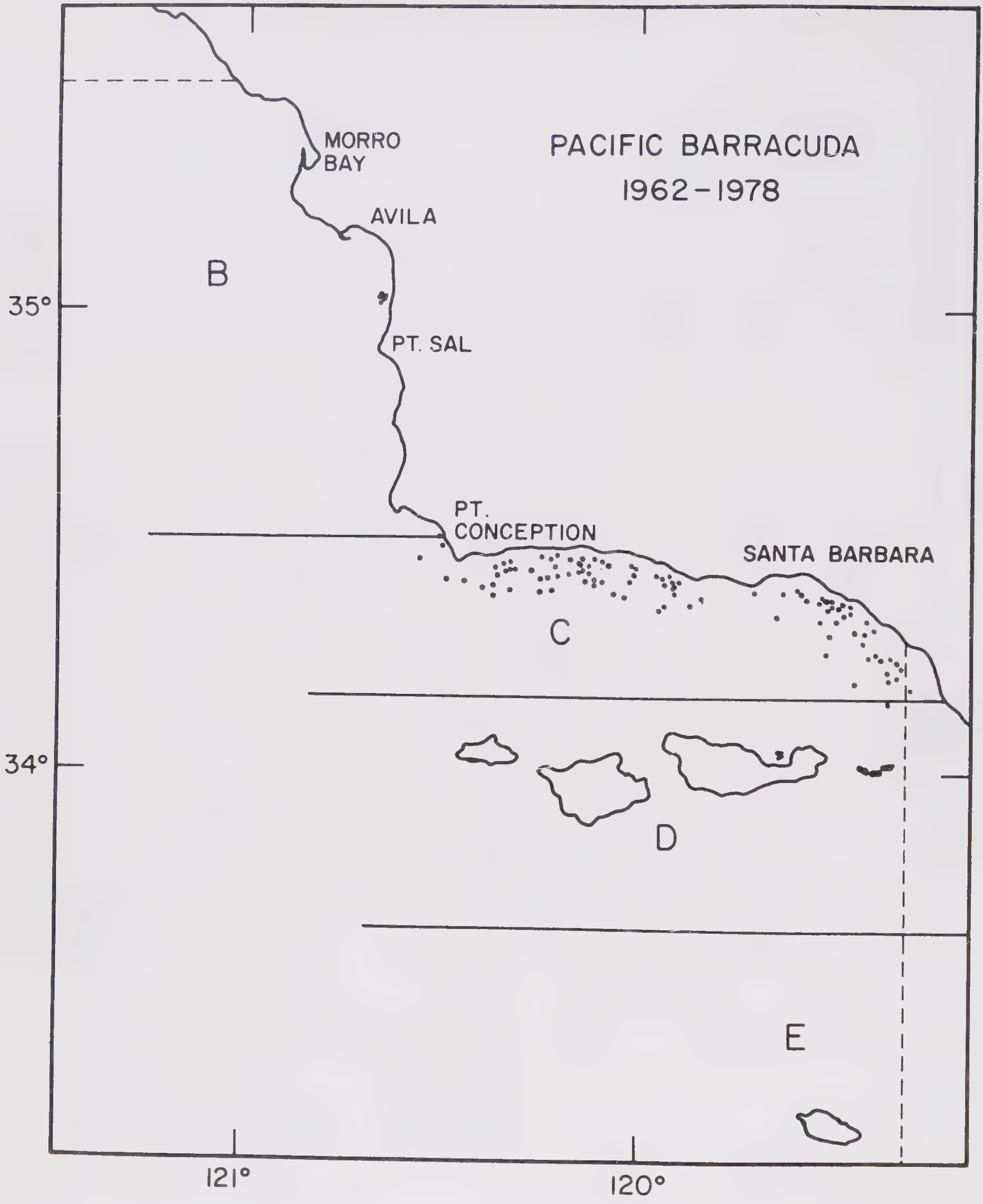

Figure 54.—Pacific barracuda—location of centers of sighting for school or school groups, Morro Bay to San Nicolas Island, 1962-78.

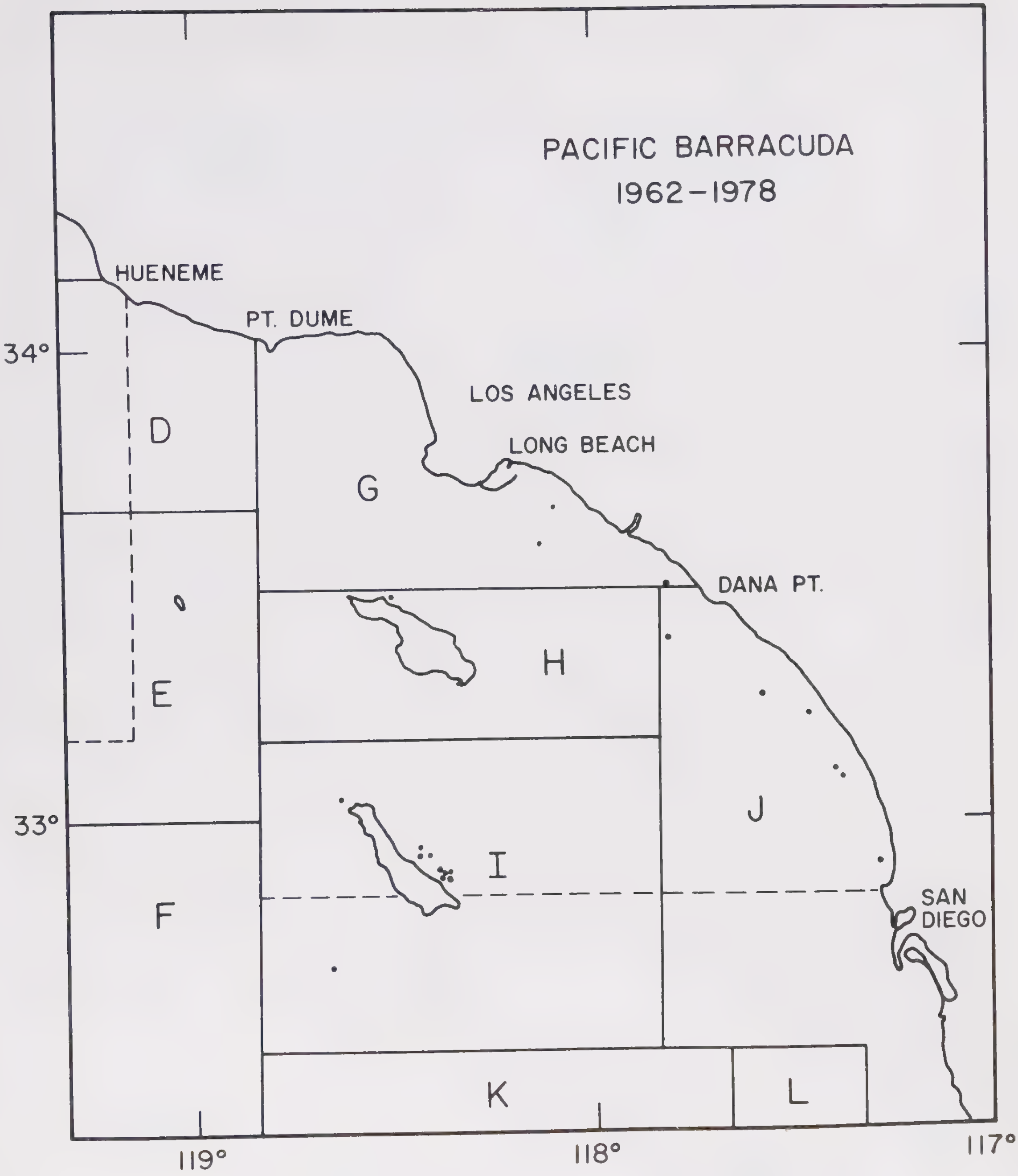

Figure 55.—Pacific barracuda—location of centers of sighting for school or school groups, Pt. Hueneme to San Diego, 1962-78.

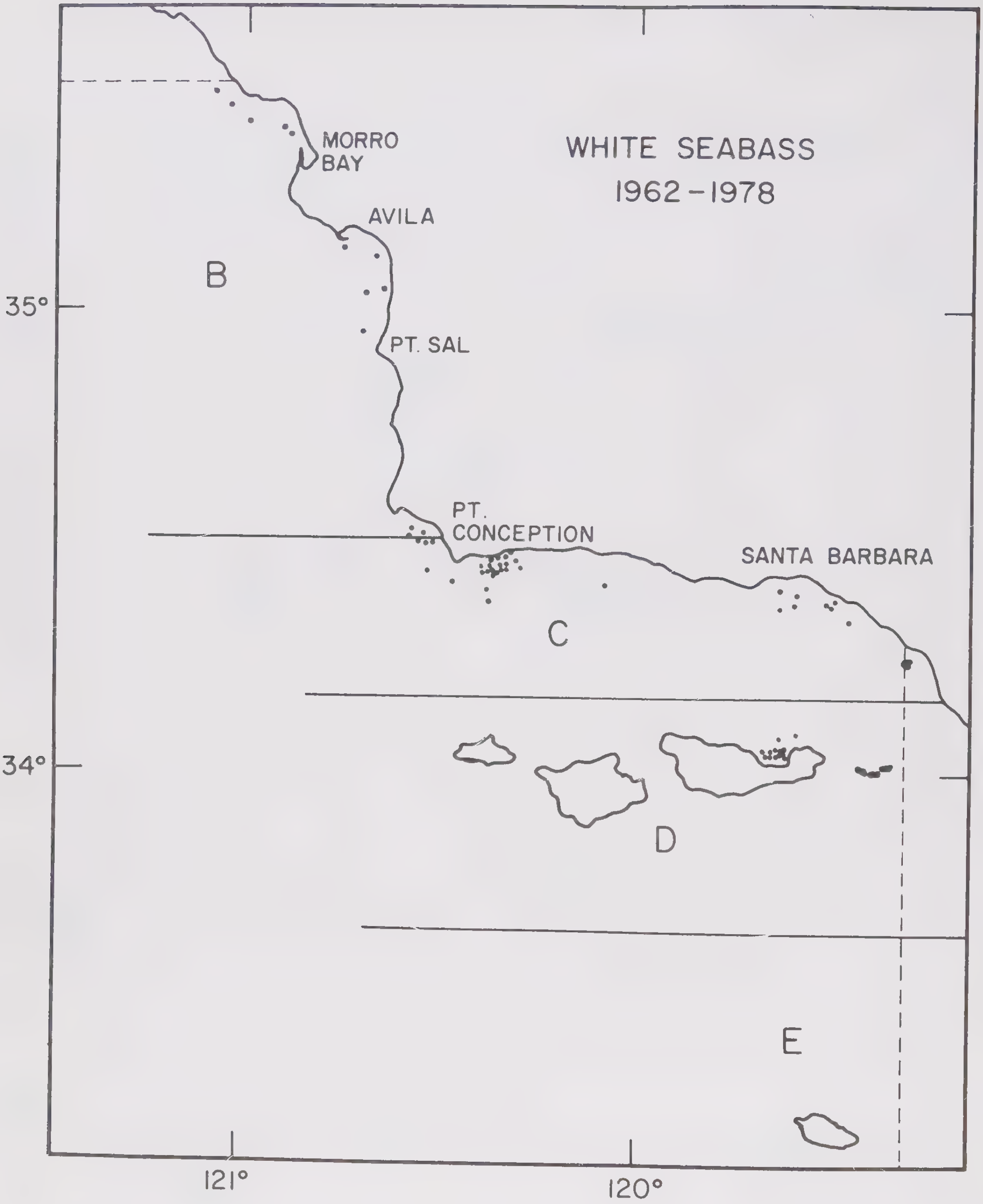

Figure 56.—White seabass—location of centers of sighting for school or school groups, Morro Bay to San Nicolas Island, 1962-78.

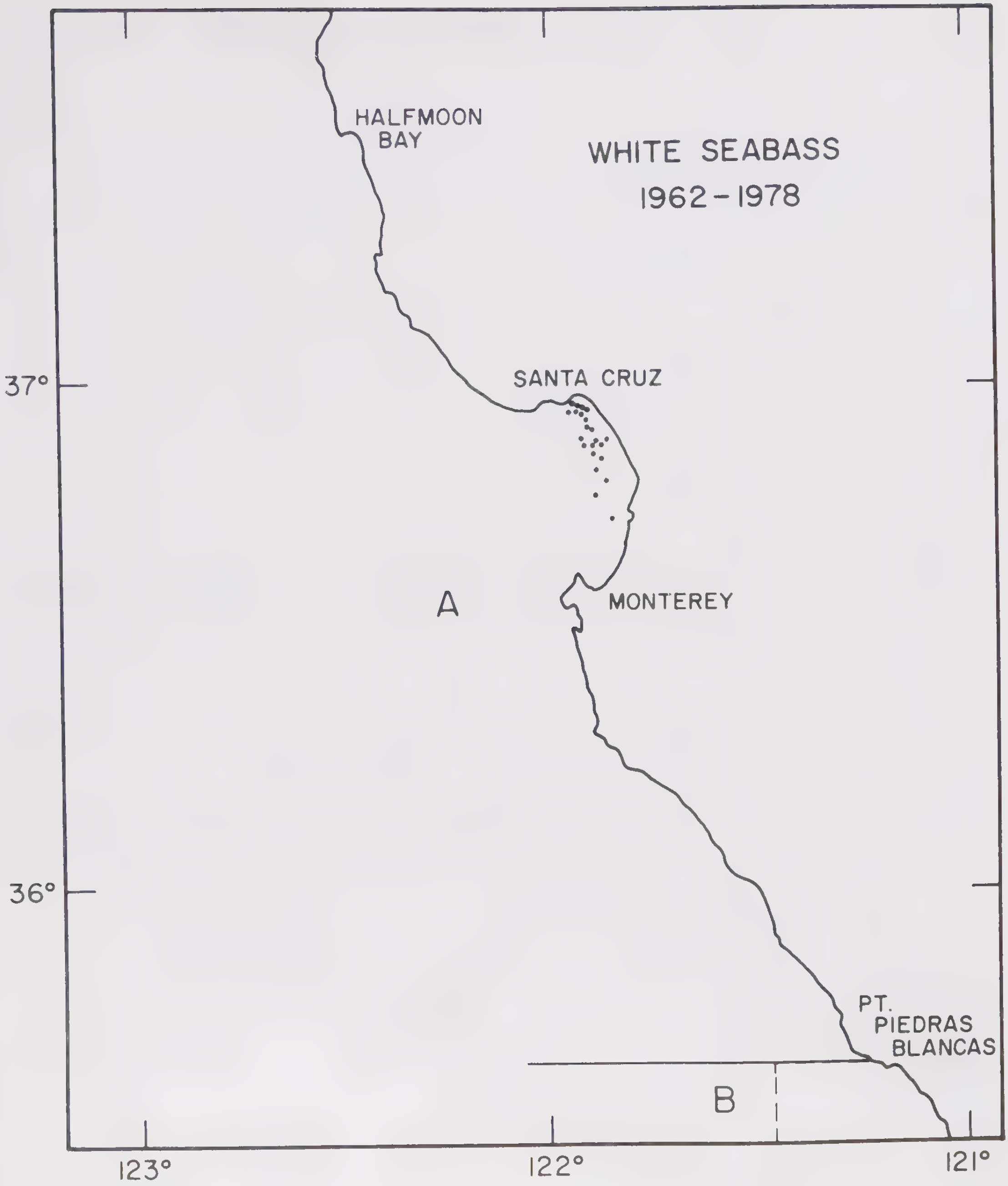

Figure 57.—White seabass—location of centers of sighting for school or school groups, Half Moon Bay to Pt. Piedras Blancas, 1962-78.

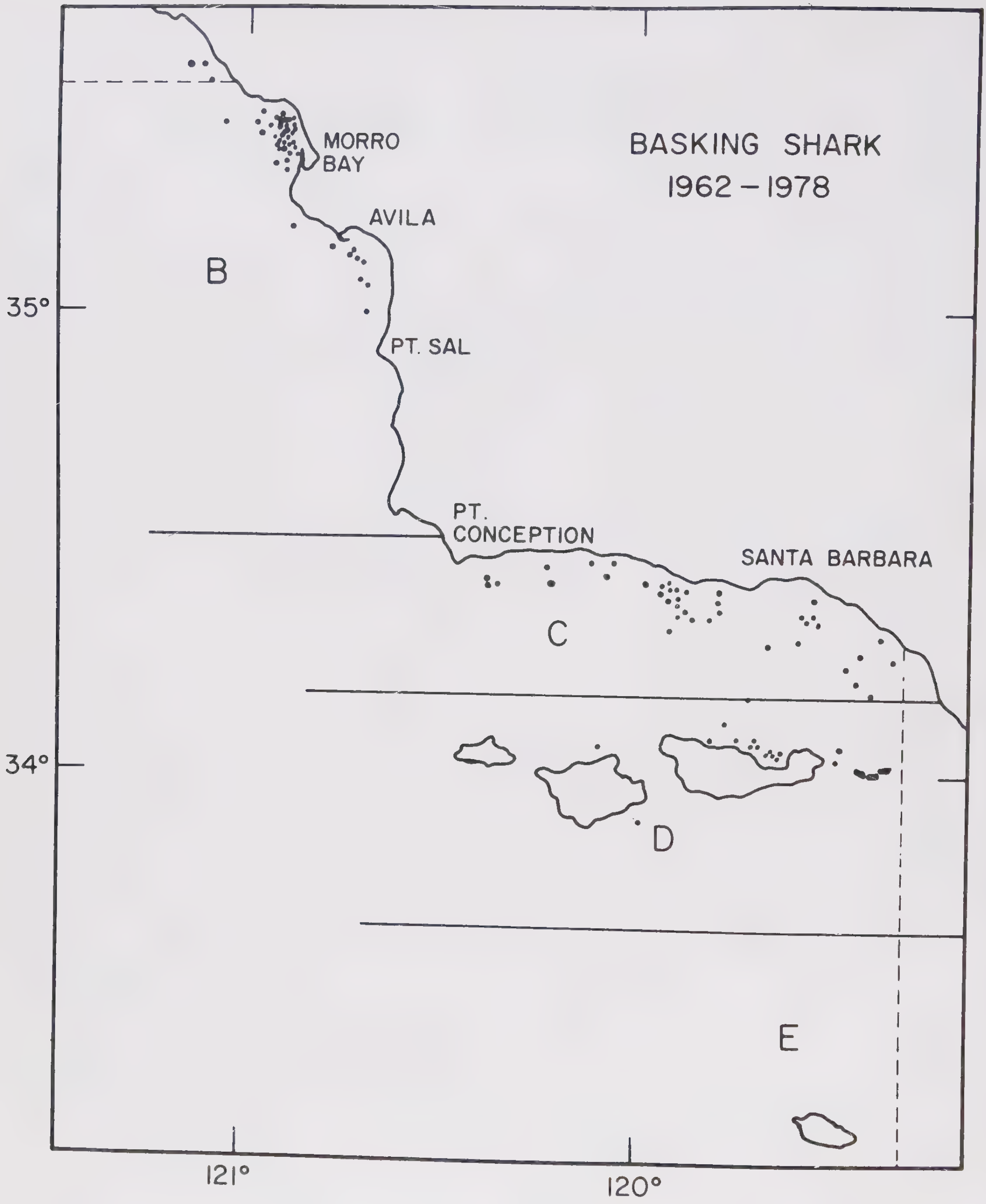

Figure 58.—Basking shark—locations of sighting one or more animals, Morro Bay to San Nicolas Island, 1962-78.

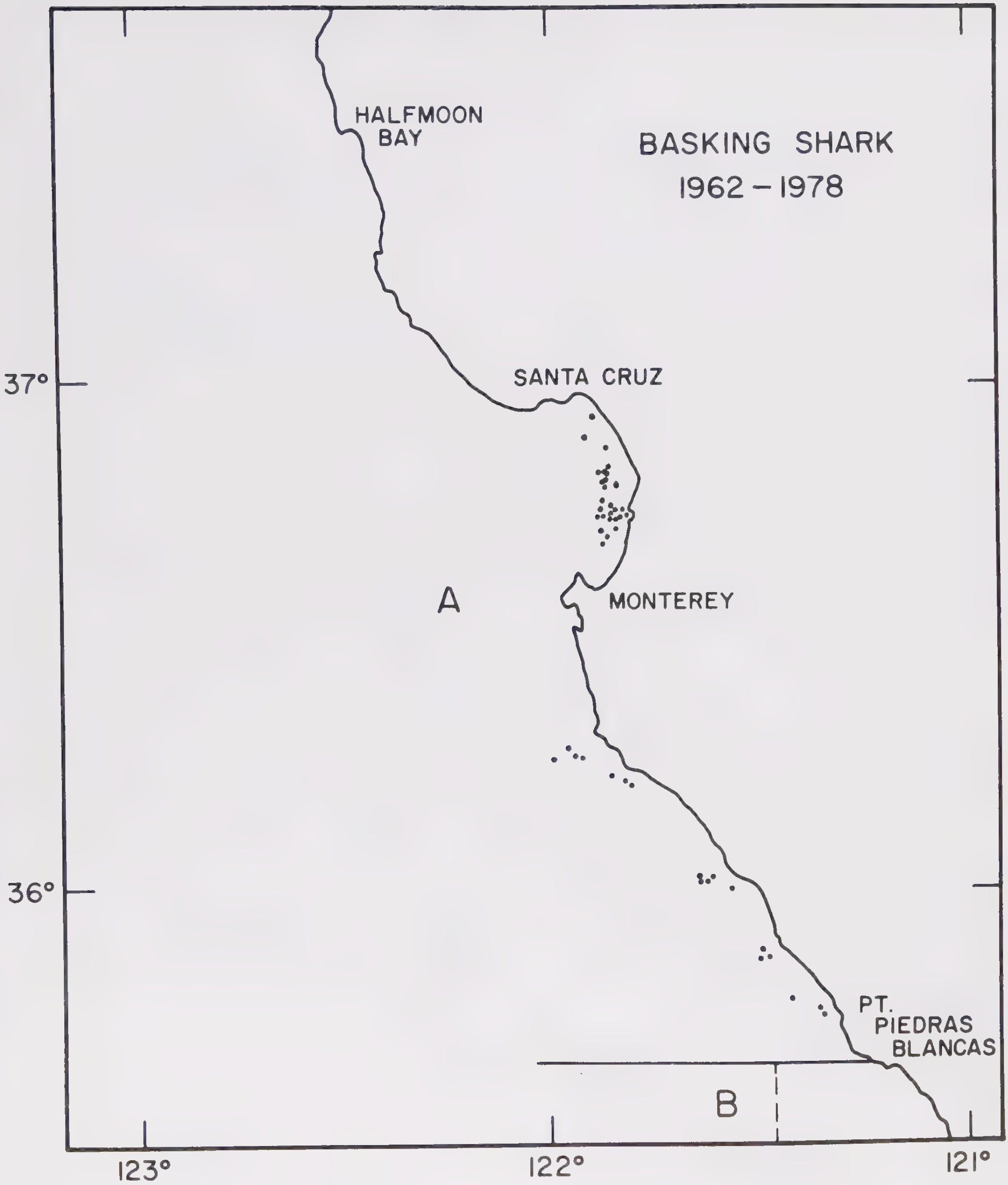

Figure 59.—Basking shark—locations of sighting one or more animals, Half Moon Bay to Pt. Piedras Blancas, 1962-78.

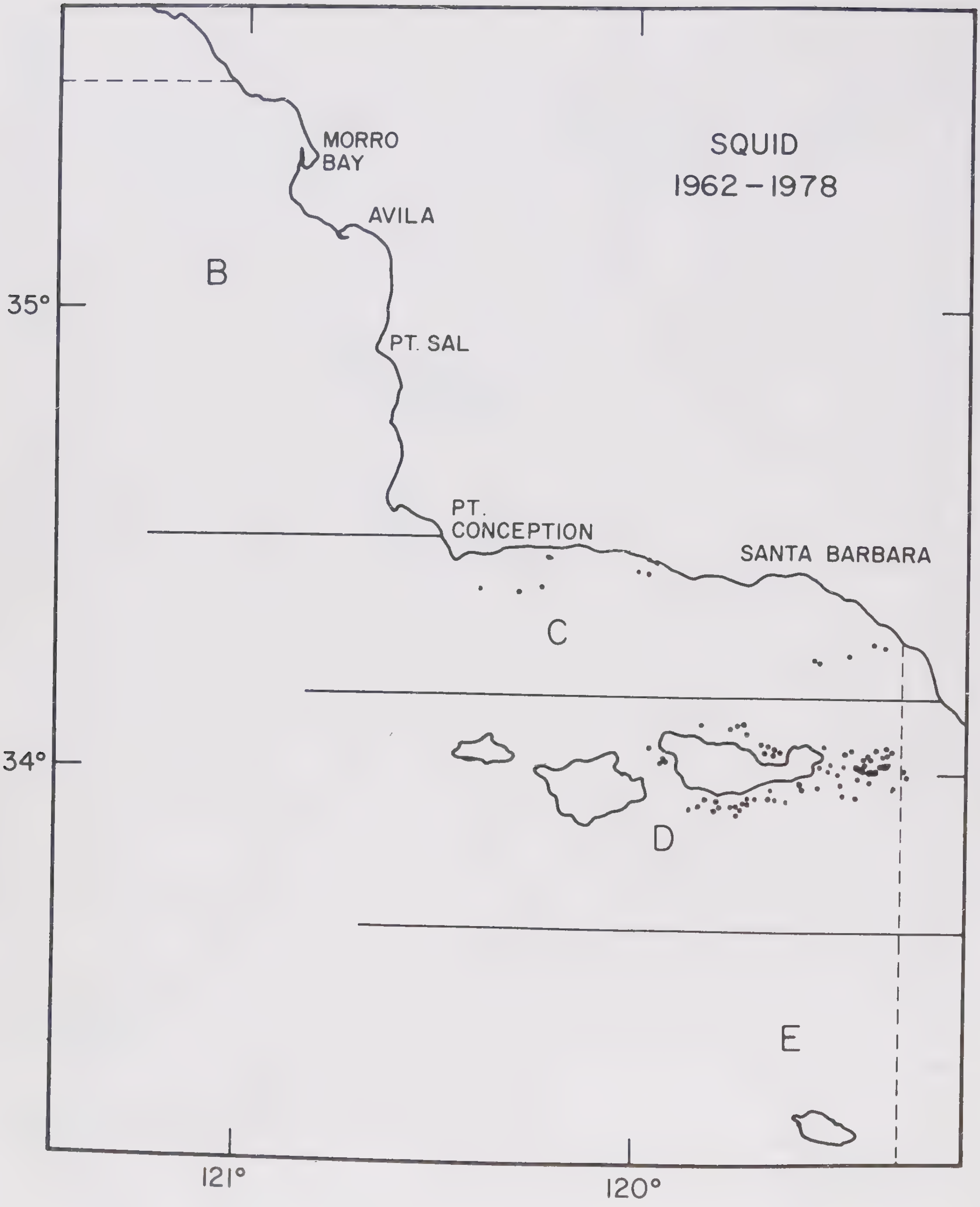

Figure 60.—Squid—location of centers of sighting for school or school groups, Morro Bay to San Nicolas Island, 1962-78.

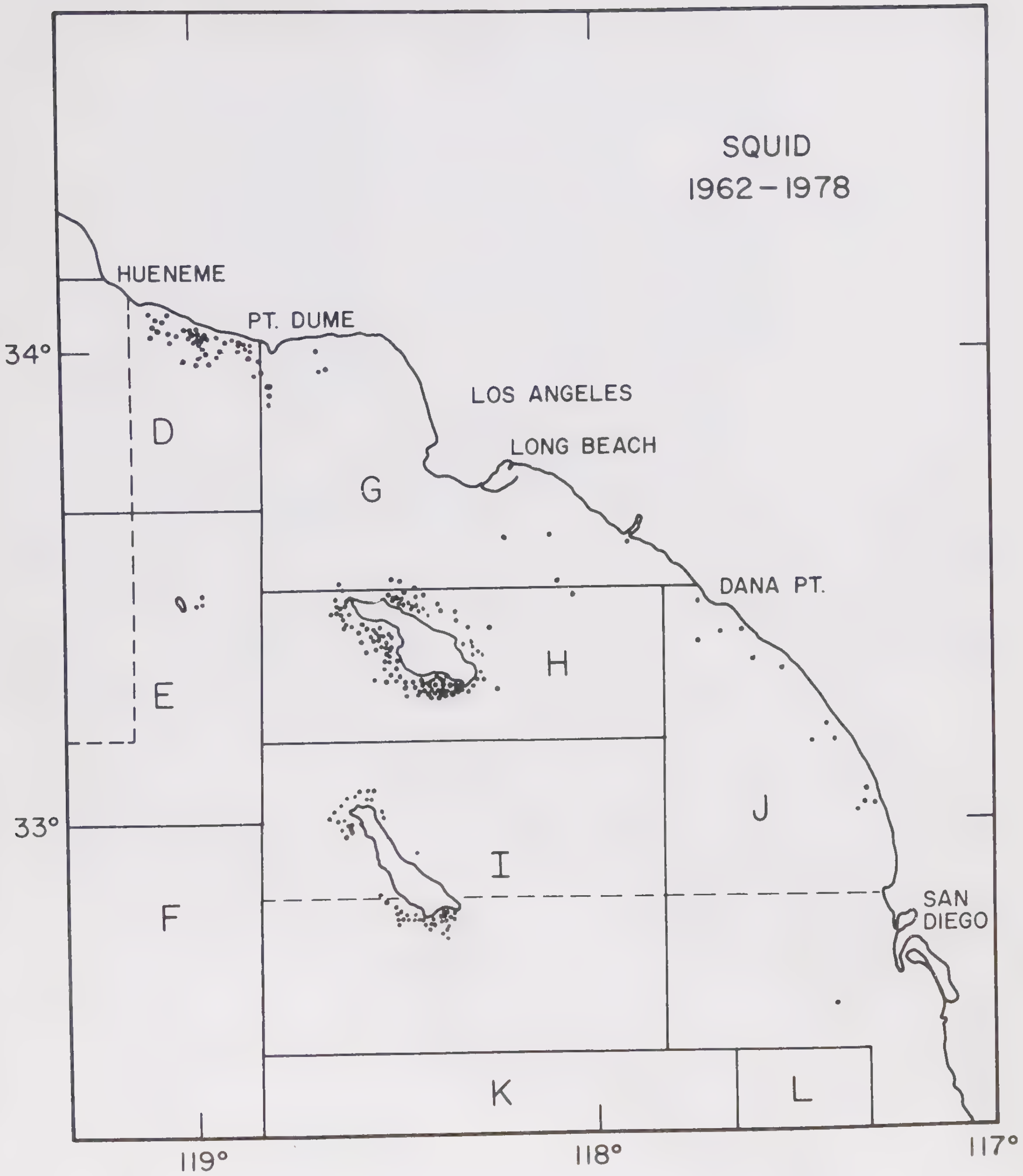

Figure 61.—Squid—location of centers of sighting for school or school groups, Pt. Hueneme to San Diego, 1962-78.

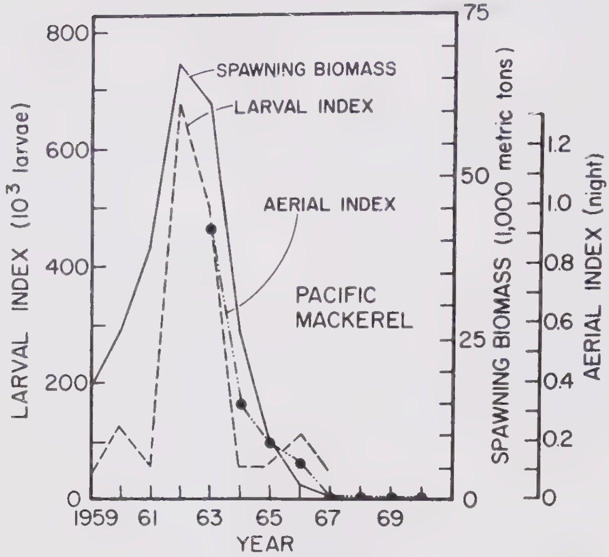

Figure 62.—Three independent estimates (spawning biomass, larval index, and aerial index) of Pacific mackerel abundance.

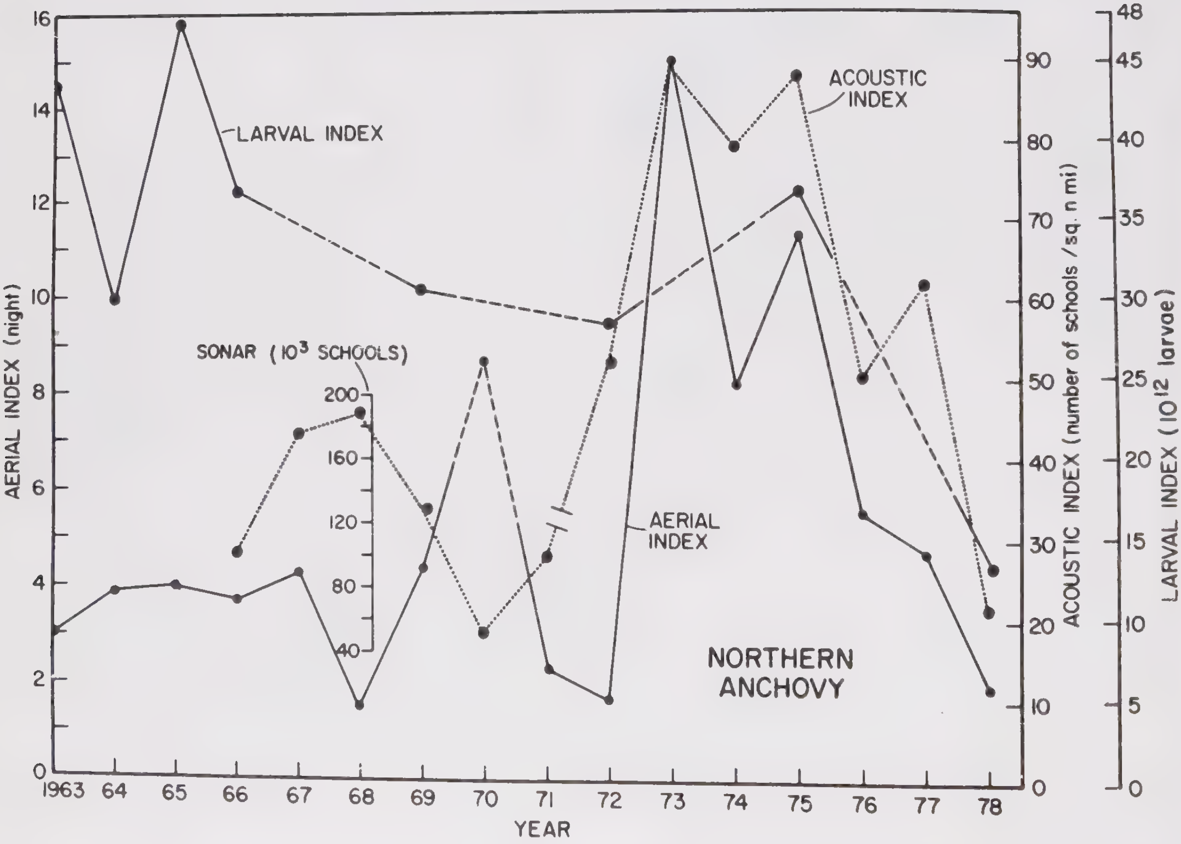

Figure 63.—Aerial, larval, and acoustic indices for the northern anchovy. Aerial night index in arbitrary units, acoustic index in schools per square nautical mile, and larval index in 10^{12} larvae.

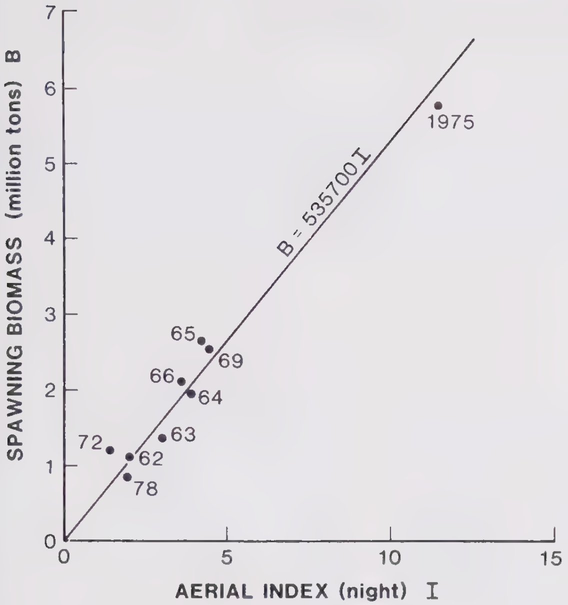

Figure 64.—Comparison of the anchovy aerial index (night) and the anchovy spawning biomass.

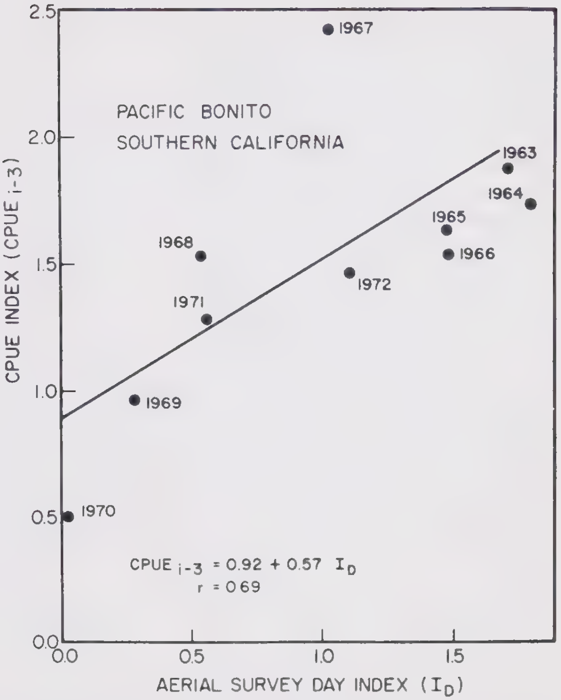

Figure 65.—Regression of aerial survey day index for Pacific bonito against partyboat CPUE index 3 yr earlier. Comparison data is for observations off southern California only.

Warm Water and Southern California Recreational Fishing: A Brief Review and Prospects for 1983

JAMES L. SQUIRE, Jr.

In June 1982 anomalous warming of the Pacific Ocean equatorial area was detected and in the months following, this warming has intensified. The periodic warming of the eastern Pacific Ocean in the equatorial area is called an "El Niño," and this warming in turn results in effects on climate and fisheries. In the past, El Niños have occurred in 1891, 1925, 1931, 1941, 1957-1958, 1972-1973 and 1976-1977.

Recent data (March 1983) show sea surface temperatures (SST's) of up to and slightly greater than 3.0°C (5.4°F) above the 20-year temperature mean in the equatorial area. Figure 1 shows the isotherm patterns and temperatures for the equatorial area. The largest recent El Niño occurred in 1957-58; the warming in the eastern tropical Pacific spread into the northeast Pacific and appears to be associated with substantial changes in fish catches by the recreational fishery off southern California.

Off southern California in 1957-58 above average temperatures were noted from January 1957 to June 1958 (18-month period), with temperatures of 4-6°F+ above the long-term mean observed in August and September 1957. Warm water periods have also occurred in 1972-73 and 1976-77; however, the magnitude and persistency of these warm water episodes was less intense than that observed for 1957-58. The 1972-73 episode had more effect on sea surface temperature in the northeast Pacific than did the one of 1976-77, exhibiting about twice the intensity. The major effects of the 1972-73 warming in the equatorial area were evident from about June 1972 through March 1973 (10-month period). The 1976 warming lasted from about June 1976 through March 1977 (10-month period).

The relation of this warming of sea surface temperatures off southern California and the offshore areas in the northeast Pacific is not well understood. Off southern California in 1972-73, above-normal temperatures were noted from January 1972 through March 1973 (14 months) with temperatures of greater than 4°F above normal noted in October 1972. In 1976, temperatures off southern California, offshore and to the southwest were greater than normal from June 1976 through April 1977 (11 months); however, only temperatures of slightly greater than 2°F above normal were recorded.

The dramatic El Niño warming now occurring in the equatorial area started in mid-1982 and has caused a sharp rise in sea surface temperatures in the area from off Peru west to the international dateline (long. 180°), more or less simultaneously. Associated with this appears to be a warming off the northeast Pacific coast to temperatures higher than the 20-year mean. Figure 2 shows the sea surface temperature chart for 16-31 March 1983 and Figure 3 is an anomaly chart showing temperatures above and below the 20-year mean for the same period.

Off southern California, current temperatures (16-31 March 1983) are 2°F above the mean, about the same level of increase as observed since November 1982. The extent of warming (amount of area that is warmer than the mean) increased in January 1983 and has remained about the same through February and into March 1983.

History indicates that with the anomalous warm temperatures off the west coast such as occurred in 1957-58, fish species more common to the tropics move into the waters off southern California and further north. Dolphin or mahi-mahi, *Coryphaena hippurus*; bullet mackerel or bullet tuna, *Auxis rochei*; shortbill spearfish, *Tetrapturus angustirostris*; finescale triggerfish, *Balistes polylepis*; middling thread herring, *Opisthonema mediastre*; spiny boxfish or trunkfish, *Ostracion diaphanum*; pilotfish, *Naucrates ductor*; and green jacks, *Caranx caballus*; are some of the species rarely observed off California, except during the warm periods. During past El Niño events, many species common to California were observed far to the north of their normal range: Pacific barracuda, *Sphyraena argentea*, were taken off the Farallon Islands (off San Francisco); white seabass, *Atractoscion nobilis*, caught off Juneau, Alaska; bluefin tuna, *Thunnus thynnus*, off Vancouver Island, B.C.; yellowfin tuna, *Thunnus albacares*, off Monterey Bay, Calif.; and skipjack tuna, *Euthynnus pelamis*, taken off Pt. Arguello, Calif.

Although the occurrence of these species in the more northern latitudes is of scientific interest, and might provide some angling opportunities not normally available, the fishermen operating off southern California are interested in what effect El Niño might have on the fish catch.

Higher sea surface temperatures and the associated changes in both the physical and biological environment cause the marine environment to shift northward, bringing the important commercial and sport species associated with it. The reverse condition also occurs: During cool water years the total environment shifts southward, though this phenomenon

James L. Squire, Jr., is with the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

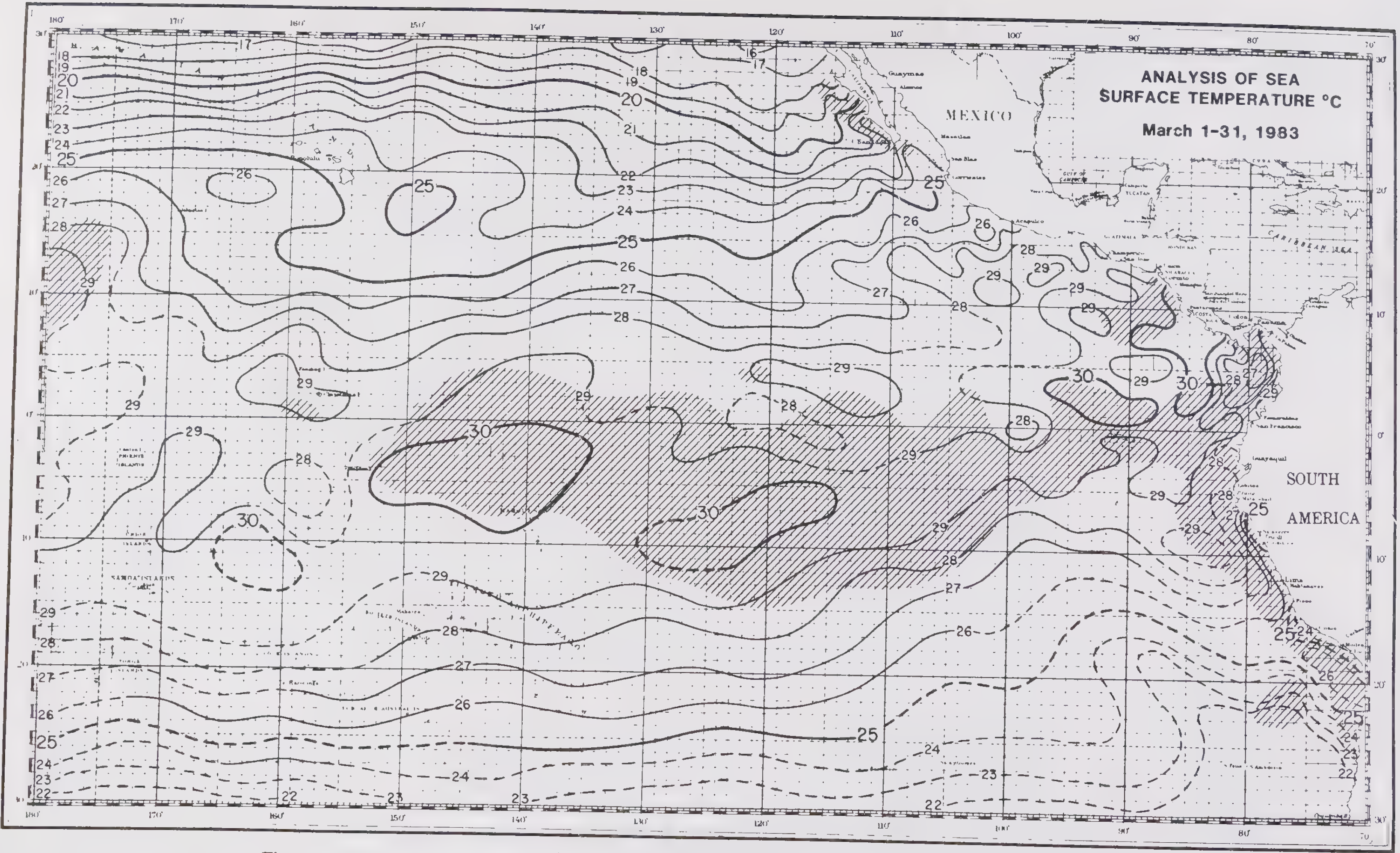

Figure 1.—Sea surface temperatures for the eastern tropical Pacific, 1-31 March 1983. Hatching indicates areas 2°C or greater above normal.

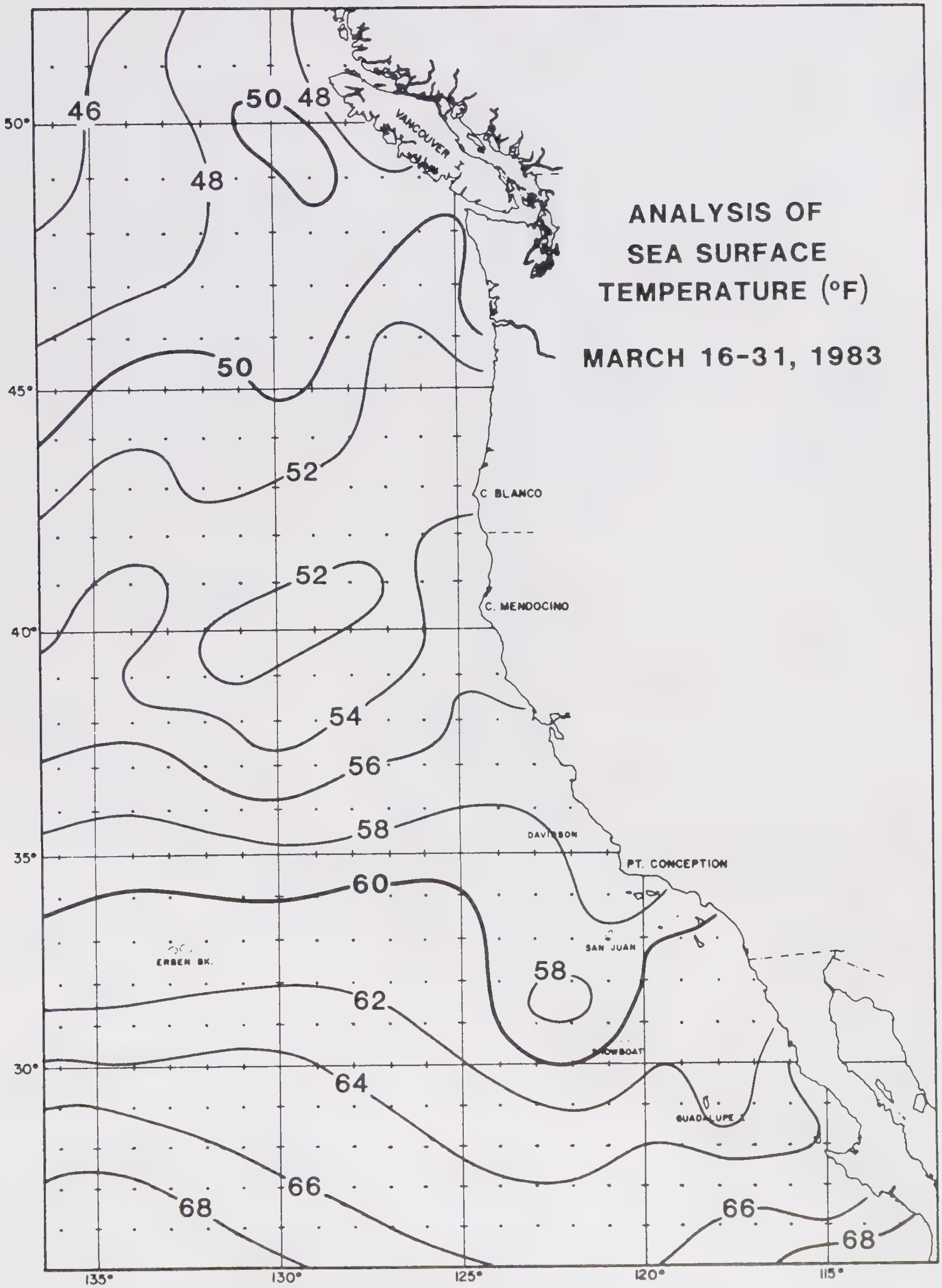

Figure 2.—West coast sea surface temperatures, 16-31 March 1983.

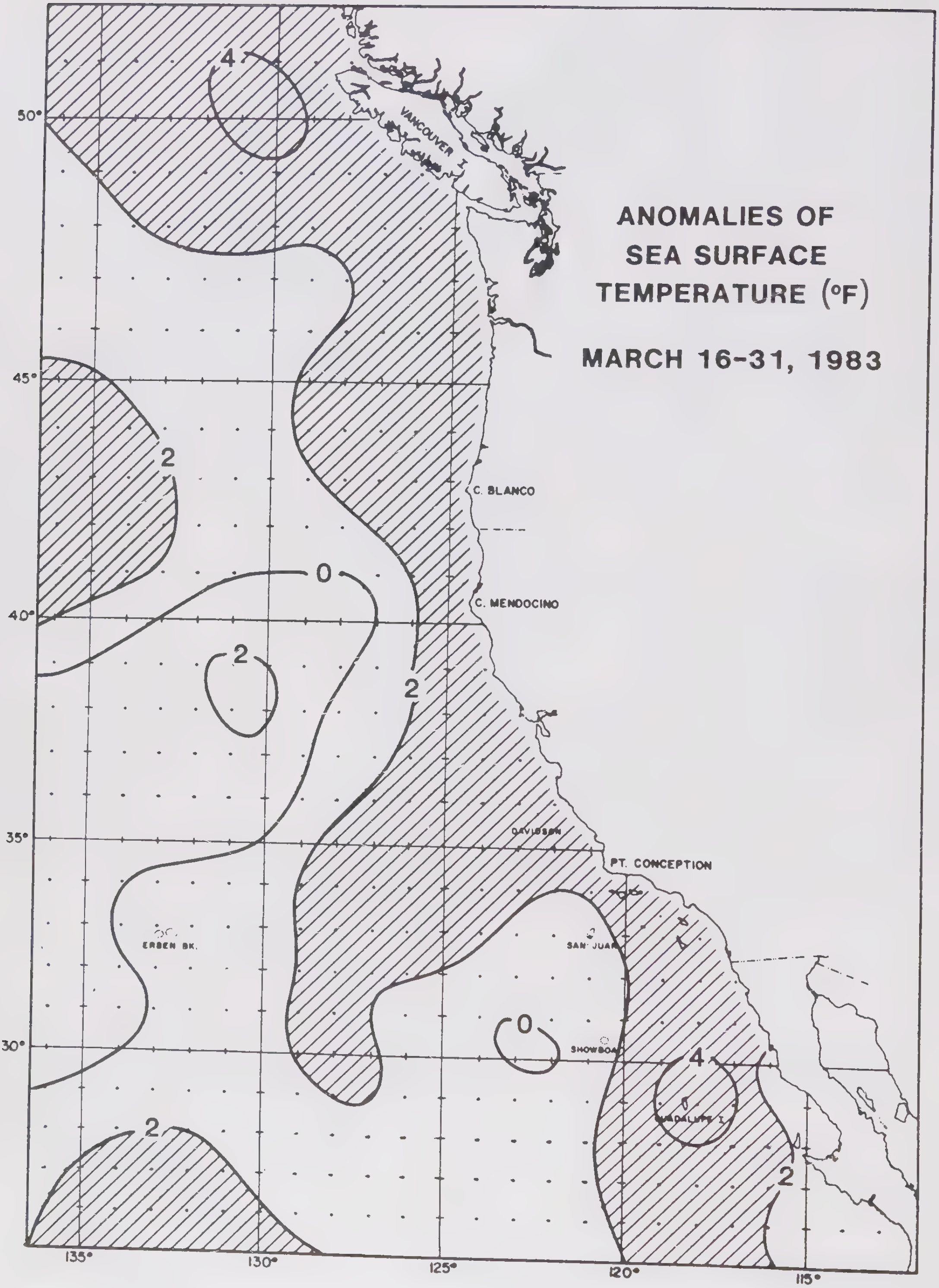

Figure 3.—West coast sea surface temperature anomalies for 16-31 March 1983. Hatching indicates areas 2 °F or greater above normal.

appears to create less interest than warm water periods.

Considerable information is available on optimum catch temperatures off southern California for such species as yellowtail, *Seriola lalandei*; Pacific bonito, *Sarda chiliensis*; Pacific barracuda; albacore, *Thunnus alalunga*; white seabass; and striped marlin, *Tetrapturus audax*, some of the more desirable commercial and sport species. The results of fishing for these important species during previous warm water years are available from historical records, which could offer an indication of the quality of fishing that might be expected during the 1983 fishing season, providing conditions similar to those observed in 1957-58 continue to develop off the northeast Pacific coast in 1983.

The catches for the following species relative to catches during warm periods are reviewed as follows: Recreational sport fishing boat and commercial catches for the years preceding the warm years of 1957-58, 1972-73, 1976-77 and 1-2 years following the warm period were examined (Fig. 4a-f). Data would indicate the following changes for species of yellowtail, Pacific bonito, white seabass, Pacific barracuda, albacore, striped marlin, and swordfish, *Xiphias gladius*. In addition, comments are given regarding the recreational fishing possibilities for skipjack tuna, dolphin, northern anchovy, *Engraulis mordax*; Pacific sardine, *Sardinops sagax*; and chub or Pacific mackerel, *Scomber japonicus*.

Yellowtail (Fig. 4a)

The area near Coronado Islands, Mexico, is the major sportfishing site for this desirable sport species. Yellowtail are also frequently taken near the kelp beds off Pt. Loma, Calif., north to La Jolla, Calif.; near Catalina Island; and sometimes off the Palos Verdes peninsula near Los Angeles, Calif.

One of the first indications of the strong warming period of 1957-58 was the excellent catch of yellowtail made at the Coronado Islands in March 1957, a fishery which normally peaks in late May or early June. Catches increased from 29,000 fish in 1956 to

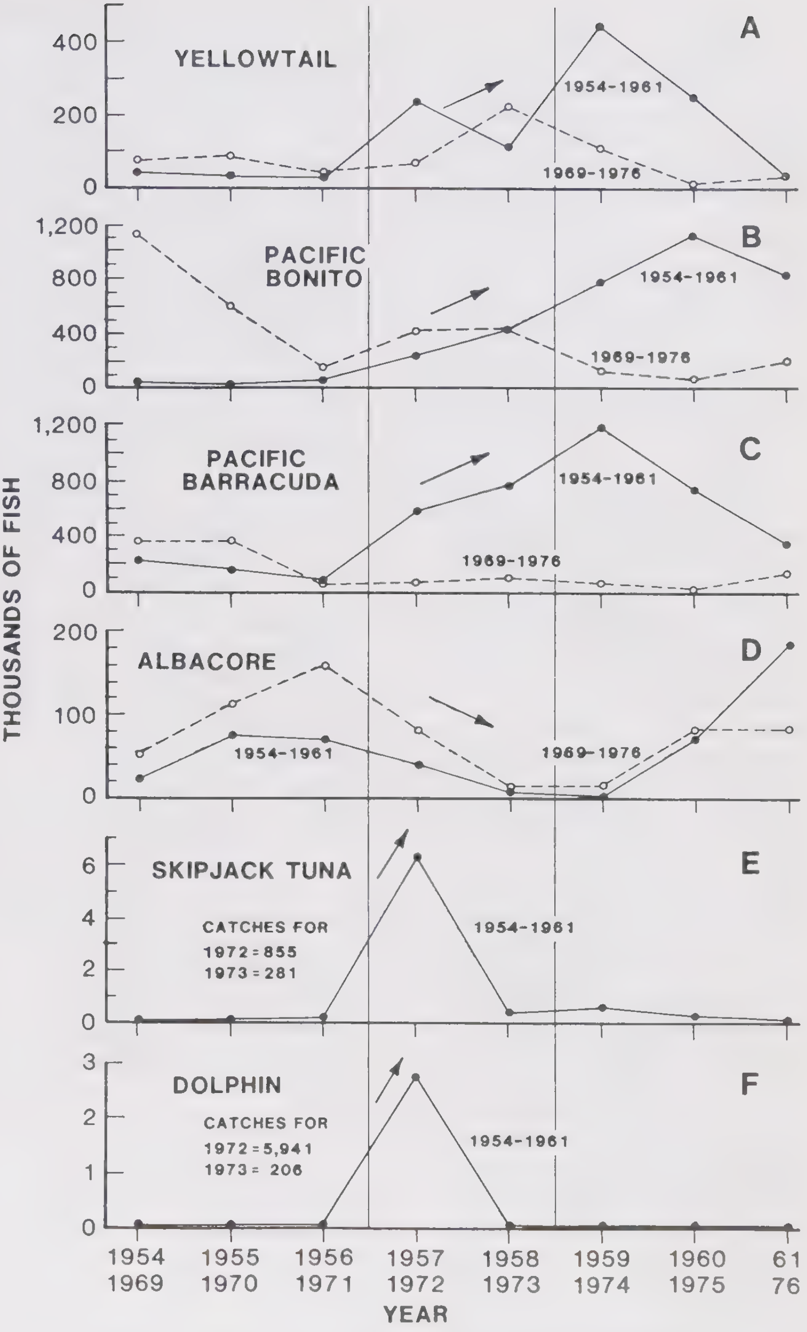

Figure 4.—California commercial sportfishing boat catches during warm water periods.

243,000 in 1957, an eightfold increase. The catch per angler day also increased from 0.49 fish/angler day in 1956 to 1.9 fish/angler day in 1957, a fourfold increase in catch rate. The 1957 total catch was 3 times greater than the 20-year mean catch for the period 1947-67 (77,000 fish). Catches declined to 123,000 fish in 1958, still well above the 20-year mean, but increased sharply to a record high of 457,000 fish in 1959, 6 times greater than the 1947-67 mean catch. Catch rates were down slightly in 1958 (1.3 fish/angler day) but increased in 1959 to an all-time record of 4.3 fish/angler day.

During the warm period of 1972-73, yellowtail catches increased from 44,000 fish in 1971 to 59,000 fish in 1972. The angler catch rate increased from 0.32 fish/angler day (1971) to 0.45 fish/angler day in 1972. The period following the warm year (as observed during the 1957-58 period) produced a greater catch. The warm period ended in March 1973, but the catch increased to a 221,000 fish total in 1973, an increase of 3.7 times the 1972 catch. The angler catch rate increased from 0.45 fish/angler day in 1972 to 1.4 fish/angler day in 1973.

The 1976 warm period, a much weaker episode than that observed in 1957-58 or 1972-73 saw only a small increase, from 19,000 fish in 1975 to 28,000 fish in 1976. Catches continued to increase in 1977 to 34,000 fish and to 38,000 fish in 1978.

Pacific Bonito
(Fig. 4b)

From 1947 to 1956 the average annual catch of Pacific bonito was 24,000 fish. In 1956, the year prior to the 1957 warm year, the catch totaled 61,000 fish. In 1957 a fourfold increase was noted, to a catch of 259,000 fish. An increase in catch was again noted in 1958 and for several years following the warm period. In 1958 the catch was 423,000 fish, increasing in 1959 to 776,000 fish, then further increasing to a record high of 1.2 million fish in 1960, thereafter declining to a catch of 806,000 fish in 1961. The catch/angler day also increased sharply. In 1956 it was 0.12/angler day increasing in 1976 to 0.48/angler day. Further increases occurred in 1958 (0.82 fish/angler day) 1959 (1.39), and 1960 (2.32).

Prior to 1972 the Pacific bonito catch in southern California had been declining. In the warm year of 1972 the catch increased from 153,000 fish to 419,000 fish. Again the catch continued to increase following the warm period and the catch in 1973 totaled 473,000 fish. The bonito catch declined in 1974.

In 1976 records indicate a catch increase to 197,000 fish from 80,000 fish caught in 1975. The catch in 1977 increased to 161,000 fish and increased again the year following the warm period (1978) to 316,000 fish.

Pacific Barracuda
(Fig. 4c)

The warm years of 1957-58 had a pronounced effect on the catch of Pacific barracuda. Catches were 6.5 times greater, increasing from 88,000 fish in 1956 to 577,000 fish in 1957. Catches further increased (by 1.4 times) in 1958 to 783,000 fish. The barracuda catch increased the year following the warm period (similar to the bonito and yellowtail catch), to a record high of 1.2 million fish. In the years 1953-56 the angler catch rate was 0.2 to 0.3 fish/angler day; in 1957 this increased to 0.82, in 1958 to 1.35, and to a high in 1959 of 1.9 fish/angler day. In 1960 the catch declined to 755,000 fish, then further declined to 392,000 fish in 1961.

Albacore
(Fig. 4d)

The recreational fishery catch of albacore appears to be negatively affected by the major warm water periods. During the 1947-67 period, the mean catch of albacore was 81,000 fish. In 1957-58 the albacore catch declined to 42,000 fish in 1957, when compared with a 66,000 fish catch in 1956. In 1958 the catch further declined to 6,000 fish, a fourteenfold reduction from the 1947-67 mean. Catches continued to decline in the year following the warm period (1959) to an all-time record low of 39 fish. Catch increased the following year (1960) to 76,000 fish, near the 20-year average, then increased again in 1961 to 185,000 fish.

Prior to the warm year of 1972 catches totaled 160,000 fish (1971). In 1972 catches declined to 87,000 fish. They further declined in 1973, the season following the warm period, to a catch of 10,000 fish. Catches increased slightly in 1974 to 12,000 fish, then rose sharply to 81,000 fish in 1975.

During the weak El Niño period of 1976 and the related warming in the northeast Pacific, little change occurred in the albacore catch. Catches were 82,000 in 1975, 85,000 in 1976, declining to 70,000 in 1977, and then increasing the year following the warm period (1978) to 93,000 fish.

White Seabass

Prior to the 1957-58 warm period, about 19,000 fish were landed in 1956. In 1957 the catch remained about the same as in 1956 (19,000 fish). However, in 1958 the catch increased to 34,000 fish, a 44 percent increase. The catch/angler day also increased in 1958 from 0.03 in 1956 and 0.02 in 1957, to 0.05 in 1958. The year following the warm period (1959) evidenced a decline in catch to 10,000 fish and a decline in catch/angler day to 0.01 fish.

By 1972 the stocks of white seabass were much reduced and a reduction in catch from about 5,000 fish in 1971 to 4,000 fish in 1972 was recorded. Catches increased in 1973 to 7,000 fish then declined in 1974 to 4,000 fish.

Striped Marlin

The long-term average catch of striped marlin off southern California is about 850 fish per year. In 1956 the catch was about 700 fish. In 1957 (the first year of the warm period) there was a slight decline in catch to 600 fish. The remainder of the warm period (1958) saw a large increase in catch, totaling 1,700 fish. The year after the warm period (1959) the catch increased to an all-time record high of

2,300 fish, then declined in 1960 to about 700 fish.

In 1972 little change was evident between catches in 1971 and 1972 (about 500 fish each year). Catches declined in 1973.

In 1976 catches declined from about 700 fish in 1975 to 350 fish, then increased to about 300 fish in 1977.

Swordfish (Commercial Catch)

The historical mean commercial catch of swordfish off California is about 4,500 fish or about 421 metric tons (t) per year. During the warm period of 1957-58, an increase in swordfish catch was observed. In 1954, a low catch (50 t ±) was recorded; catches increased in 1955 to about 150 t and increased again in 1956 to 180 t. Catches increased to 210 t in 1957, and to 280 t in 1958; they then declined slightly in 1959 and 1960.

For the warm periods of 1972 and 1976, catches were at or near low points. The 1972 catch was 180 t, up only 70 t from a low point observed in 1971. The 1976 catch was a low point in catch, 80 t.

Possible Effects on Other Species

In addition to the species listed there is considerable interest in other species associated with the recreational and commercial fisheries off southern California.

Pacific Sardine

The Pacific sardine resource appeared to have greater success during warm year periods (successive years of slightly warmer water). A small reduction in larval mortality during the 1957-58 period was suggested by the data. Spawning was shifted northward during the warm period. Spawning during the warm period of 1957-58 did not result in a large increase in year-class strength.

Northern Anchovy

Fluctuations in landings of the northern anchovy were market-related during the warm years of 1957-58. In 1956, commercial landings were 28,000 tons, declining in 1957 to 20,000 tons, and in 1958 to 6,000 tons. Reports on the anchovy fishery indicate this reduction was due to economic conditions, and an upsurge of sardine availability in 1958. Census estimates show an increase in the numbers of anchovy larvae in the years 1956 through 1958. The bait fishery showed a decline in catch, dropping from 6,000 tons in 1956 to 4,000 tons in 1957 and 1958. Warm water periods appear unfavorable to the inshore live-bait anchovy fishery.

The commercial reduction purse seine fishery appeared not to be greatly affected by the 1972-73 warm period. Catches for the period 1970 through 1973 were 96,000, 44,000, 69,000, and 132,000 tons per year, respectively. However, the aerial index of apparent abundance determined from the flight logs of commercial aerial fish spotters was low in 1972, declining from a high in 1970. This would indicate that the northern anchovy was less available in the commercial fishing areas in 1972, but not to the extent that commercial catches were reduced. The aerial abundance index increased sharply to a record high in 1973.

Chub Mackerel

The chub or Pacific mackerel, *Scomber japonicus*, resource's total biomass declined sharply in the middle and late 1940's and biomass fluctuated until 1964 when it dropped to a very low level. Catches of Pacific mackerel were about 55,000 tons in 1940, 35,000 tons in 1941 (an El Niño period), and 25,000 tons in 1942. Catches declined during the 1957-58 warm period from 40,000 tons in 1956 to 35,000 in 1957, and 15,000 in 1958. Catches increased in the years 1959 through 1963. The biomass of Pacific mackerel was at a very low level in 1972 and no changes were detected. In 1976 the aerial index of apparent abundance increased slightly, further increasing to a high level in 1977. The influence of the warm period on this increase is not known.

Skipjack Tuna (Fig. 4e)

During the 10-year period preceding the 1957-58 warm period the average annual catch of skipjack tuna off southern California was 166 fish. In 1957 the catch increased to 6,428 fish. However, in 1958 the catch dropped to 491 fish.

Dolphin (Fig. 4f)

The largest catch for the 10-year period prior to 1957 was 15 fish (1947). In 1957 the catch was recorded at 2,805 fish, and in 1958 no catches of dolphin were recorded. Both skipjack tuna and dolphin are tropical species, and by late summer 1958 the warming period was on the decline and cooler temperatures off southern California, compared with late summer temperatures of 1957, restricted their occurrence in southern California waters. In the warm year of 1972, catches rose to a record 5,941 fish.

Summary

The warm years of the 1957-58 period were more intense, lasted longer, and had a greater effect on southern California fishing than did the warm periods of the 1970's. The sea surface temperature isotherm charts of the equatorial and northeast Pacific in January 1983 resemble closely those of January 1958. Temperatures of up to 30°C (86°F) are common to the major areas of warming during both January 1958 and 1983. If the current warm water conditions continue in 1983 through the spring and summer period, thermal conditions in the northeast Pacific not unlike those observed in 1957-58 should be evident. The 1957-58 warm period lasted about 18 months; the 1972-73 and 1976-77 periods both lasted about 1 year. At the present time we are about 9 months into a strong El Niño period. If the El Niño phenomenon and its effect on the northeast Pacific continues it will have significant effects on the 1983 and possibly 1984 catches of coastal migratory species. The following predictions are based on historical data.

Yellowtail

Catches should increase substantially in 1983 and catches as high or higher might be expected the year after the tropical warming period subsides. In 1959 an abundance of small yellowtail were taken, indicating that this species had probably spawned successfully off southern California. At the present time the yellowtail population is much reduced from levels common to the late 1950's; therefore, although catches may be higher, this will not necessarily indicate an improvement in the size of the yellowtail population.

Pacific Barracuda

Stock size is currently very small compared with that of the late 1950's. Increases in catch should be expected though the totals will not approach the catch levels of the 1950's; higher catches following the warm period could be expected.

White Seabass

Stock size is low and, though a slight increase in catch is possible in 1983, the total numbers of fish caught will remain low.

Pacific Bonito

Catches off southern California respond positively to warm periods and though the stock size is reduced, increased catches could be expected. The recreational fishery increased during the warm periods of 1957-58 and in 1972-73 peak catches are recorded one and two years after the "El Niño" period.

Prior to 1957-58 the abundance of Pacific bonito was low off southern California. The 1957-58 warm period moved bonito into the southern California Bight where they were reported to have spawned. Abundance in southern California waters remained high until 1964-65 when they became a major target species for the purse seine fishery.

Albacore

Recreational fishery catches during the warm period of 1957-58 and in 1972-73 declined substantially, reaching their lows 1 year after the warm period. This reduction in catch is not evident in the commercial catches of 1957-58, and only a small reduction in catch was recorded in 1972. The mobility of the commercial albacore fleet enables it to fish distant water areas compared with the recreational fleet.

It may be expected that the recreational albacore fishery will experience a decline in catch if the influence of the warm period is evident during the summer and fall of 1983.

Much has been written on the El Niño, an equatorial phenomenon, and its effects on marine fishes and birds off Peru. The effects of the warm periods off California on the smaller pelagics such as the Pacific sardine, northern anchovy and Pacific or chub mackerel are not well understood. The effects on the anchovy off Peru by the El Niño are well documented; indications are that off California the inshore bait fishery for the northern anchovy has a more difficult time in warm years, although the commercial fishery may not be greatly affected. Apparently the catches of Pacific mackerel and its resource were not substantially influenced by the warm years of 1972 or 1976.

Off southern California the effects of the El Niño are evident but not to the magnitude that is seen off Peru. The important fact is that in the El Niño area, sea surface temperature anomalies of up to and slightly greater than 4°-6°C (5.40°-10.8°F) are recorded, while off southern California sea surface temperature anomalies rarely reach 3.3°C (6.0°F), or a level only slightly greater than half the increase that is observed for the El Niño area. Therefore, the fishery resources off southern California are not subjected to the extremes of temperatures as those inhabiting the eastern tropical Pacific and tend to respond less dramatically.

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Weight Frequencies for Striped Marlin, *Tetrapturus audax*, Caught Off Southern California

JAMES L. SQUIRE, Jr.

Introduction

Striped marlin, *Tetrapturus audax*, are caught by marine game fish anglers off southern California only during a brief period of the year, with most of the catch landed between 15 August and 15 October of any one year. The annual catch may range from 50 to 2,300 marlin but averages about 800. Angler catch rates are low off southern California when compared with those of other striped marlin fishing areas in the northeast Pacific, such as the area about the tip of Baja California Sur, Mexico (Squire, 1974). This area lying about 750 miles to the southeast of southern California is intensively fished by U.S. anglers (Talbot and Wares, 1975).

Catches in both the southern California and Baja California areas were sampled during 1967-70 for weight frequencies and other biological parameters by the National Marine Fisheries Service (Eldridge and Wares, 1974). The mean weight of marlin was found to be greater by about 16.8 kg (37 pounds) for landings in southern California when compared with landings near the tip of Baja California Sur, Mexico (Talbot and Wares, 1975), an area that is near the center of striped marlin distribution in the northeast Pacific.

The southern California fishery is near the northeastern limit of striped marlin distribution in the Pacific Ocean and marlin are caught in increasing numbers by this fishery during periods of sea surface temperatures of 20°C (68°F) or greater (Squire, 1974).

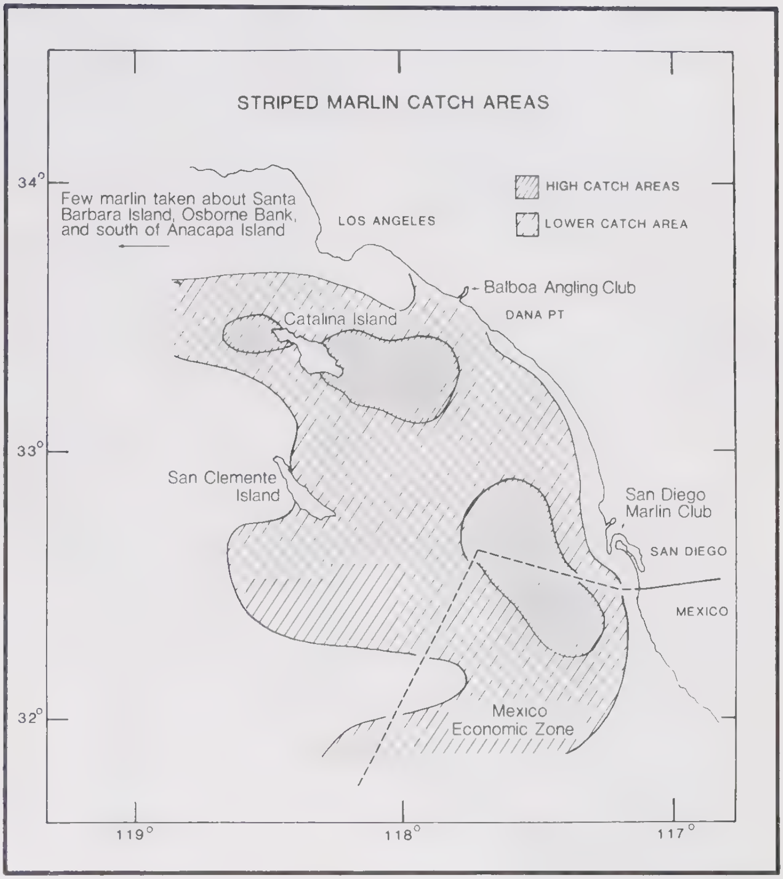

Figure 1.—Major catch areas for striped marlin off southern California.

Geographical areas within the southern California Bight yielding high catches of striped marlin may vary between years, from a fishing area to the west and southwest of San Diego to an area between the mainland near Dana Point to and about Santa Catalina Island, a range of about 90 miles. The time distribution of the catch differs slightly between the Santa Catalina Island area and the area off San Diego. Figure 1 illustrates the major fishing areas for striped marlin relative to the locations of the weigh stations from which the data used in this report were obtained.

James L. Squire, Jr., is with the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

In southern California the major locations for weighing angler-caught striped marlin are the San Diego Marlin Club, located on San Diego Bay, San Diego, Calif., and the Balboa Angling Club, located on Newport Bay, Balboa, Calif. Both clubs maintain weight records for all marlin landed, and the records compiled at these two locations represent an estimated 90 percent or more of the total southern California landings. Weights are assumed to be accurate as the marlin are weighed on scales that are certified by either the San Diego or Orange County Sealer of Weights and Measures. Marlin caught in the vicinity of Santa Catalina or San Clemente Islands are sometimes weighed at the town of Avalon, Santa Catalina Island, Calif. These marlin are frequently taken across the Catalina Channel to Newport Bay where they are reweighed by the angler at the Balboa Angling Club.

Weight frequencies from club weight records and the work of Eldridge and Wares (1974) are described. An analysis of trends in weight frequency, both by area and by year, is presented.

Data Sources

Striped marlin are usually weighed on the same day as they are caught, except for a few that are tagged and released or released on the fishing grounds. Special care, such as covering the marlin with a wet cloth or sheltering it from the elements to prevent dehydration after capture, is not usually taken. Since sea surface temperatures off the coast of southern California are in the range of 20-22°C (68-72°F) during the fishing season and offshore air temperatures are near that of sea surface temperature, the degree of dehydration before weighing is probably minimal. However, the magnitude of the weight difference between time of capture and weighing ashore is not known.

Weights are recorded in pounds of total or round weight. Marlin are not examined to determine sex so weights given in this paper represent a composite weight of both male and female marlin.

Data on the date landed and total weight are published annually in the yearbooks of both the San Diego Marlin Club and the Balboa Angling Club. Information is also included on the angler's name, boat captain, type of tackle, weight of fish, and time to land the marlin.

Weight records in this paper represent striped marlin weights for 15,138 fish. The Balboa Angling Club recorded weights for 6,620 marlin over a period of 36 years (1945-80); the San Diego Marlin Club has recorded weights for 8,518 marlin over a 21 year period (1960-80). Weight data for this review were obtained from the reports of Talbot and Wares (1975) and record books of the San Diego Marlin Club and the Balboa Angling Club. Typically, few marlin were reported weighed in July and November, and both clubs recorded the highest catch in September.

The only historical weight records of striped marlin for the early 1900's are those published by Jordan (1916) describing the average weight of 251 specimens landed at Santa Catalina Island from 1910 to 1916. For the 251 samples of "Japanese spearfish," *Tetrapturus mitsukuri*- (synonymy given by Jordan and Snyder, 1901), Jordan reported the average weight to be 82.6 kg (182 pounds). This weight would indicate mean size reduction of approximately 18.1 kg (40 pounds) when compared with the 1960-75 mean weight off southern California of 64.4 kg (142 pounds). The reduction in average weight by 18.1 kg (40 pounds) may be the result of fishing.

Weight Record Analysis

Data giving striped marlin mean weights by month and year, number of marlin in the sample and weight averages by month are presented in Table 1, for 21 years of San Diego Marlin Club data and 36 years of Balboa Angling Club data.

Figure 2 shows the percentage of landings by month for weight records compiled by the San Diego Marlin Club and the Balboa Angling Club; catch trend by month from both clubs' records were similar, with peak catches during the same month (September). Slightly higher landings (7 percent greater) were recorded for August (the beginning of the fishing season) from Balboa Angling Club records, when compared with San Diego Marlin Club records. The landing weights were slightly less (4 percent less) in the Santa Catalina Island and Channel area in November as reflected in the Balboa data compared with the San Diego area records. Effort data were not available; therefore, any catch percentage differences could be the result of variations in fishing effort.

Weights were grouped by 4.5 kg (10 pound) increments and plotted by year for data from 1945-80 for the months July through October, or by weight data for each season, to determine if any modal size groups could be observed moving through the fishery. An example of the weight structure of the catch is given in Figures 3a, b, and is typical of other years. The figures show that for 1963, a record catch year, little change is evident between weight groups during the months of July, August, September, and October. The landings weighed at the Balboa Angling Club appear to have a distribution similar to the catches landed at the San Diego Marlin Club.

Discussion and Summary

Biological research conducted at San Diego during the period 1967-70 indicated that of 462 marlin sampled, 67 percent were female. During the early part of the fishing season females were the predominant sex caught, with the sex ratio changing to about 50:50 later in the season. Females were heavier than males for a given length, and statistical tests indicate this difference to be significant (Wares and Sakagawa, 1974). Marlin landed at San Diego were heavier when compared with marlin of the same length near the tip of Baja California Sur, and at Mazatlán, Mexico, as determined by comparing weight as a function of eye (orbit) to tail fork length (Fig. 4).

There is a small difference in monthly mean weight of marlin landed at the Balboa Angling Club compared with weights recorded by the San Diego Marlin Club. The marlin weighed at the Balboa Angling Club averaged 4.1 kg (9.1 pounds) heavier in July when compared with those weighed at San Diego, 1 kg (4.5 pounds) heavier in August, 1.5 kg

Table 1.—Striped marlin mean weight by month and year as recorded from sport catches landed at the San Diego Marlin Club and Balboa Angling Club (the number of fish is in parentheses). Weight is in pounds (round weight) as recorded.

	July		August		September		October		November		
Year	No. of Fish	Mean wt.	No. of Fish	Mean wt.	No. of Fish	Mean wt.	No. of Fish	Mean wt.	No. of Fish	Mean wt.	Average weight
The Marlin Club											
1960	(3)	145.00	(96)	152.00	(276)	132.31					137.61
1961	(4)	170.00	(24)	168.33	(344)	140.47	(46)	141.73			142.50
1962	(1)	135.00	(16)	134.37	(39)	145.51	(1)	155.50			142.36
1963	(14)	136.42	(463)	136.92	(904)	132.07	(78)	116.66			132.83
1964			(95)	128.47	(422)	127.96	(371)	142.08	(79)	146.89	134.97
1965			(24)	122.29	(126)	139.44	(148)	146.48	(2)	145.00	141.58
1966	(6)	111.00	(112)	133.30	(367)	128.46	(97)	128.19	(2)	135.00	129.17
1967	(11)	124.09	(203)	122.24	(347)	121.13	(43)	131.74	(217)	145.41	128.42
1968	(12)	121.66	(43)	119.88	(331)	135.69	(146)	139.93	(59)	150.76	136.81
1969	(2)	110.00	(32)	143.75	(191)	146.30	(33)	148.93	(11)	153.18	146.33
1970	(2)	155.00	(31)	124.67	(32)	139.68	(30)	154.00	(1)	185.00	138.85
1971			(26)	137.50	(48)	147.50	(33)	146.0			144.60
1972	(2)	195.00	(17)	142.65	(75)	142.40	(29)	142.07	(2)	155.00	146.40
1973	(1)	195.00	(25)	145.40	(20)	145.50	(30)	151.30	(1)	205.00	149.14
1974	(4)	135.00	(57)	137.00	(90)	142.20	(133)	148.90	(10)	150.0	144.38
1975	(1)	175.00	(62)	150.00	(72)	152.40	(55)	152.40			151.70
1976	(1)	145.00	(10)	142.00	(63)	143.30	(60)	142.10	(5)	141.00	142.60
1977	(5)	135.00	(47)	145.76	(115)	152.48	(61)	157.30	(48)	158.75	153.21
1978	(3)	158 33	(40)	142 25	(148)	147 64	(239)	148 26	(75)	150 73	148 03
1979	(4)	135.00	(92)	144.13	(149)	141.11	(58)	152.50	(42)	156.43	145.62
1980	(3)	171.67	(185)	146.62	(198)	148.43	(123)	148.17	(14)	144.29	147.75
21-year mean	(79)	137.10	(1,700)	137.52	(4,357)	135.70	(1,814)	143.61	(568)	149.15	
Balboa Angling Club											
1945			(53)	138.58	(84)	137.97	(3)	121.66			137.85
1946			(82)	142.19	(91)	140.76	(13)	146.53			141.80
1947			(30)	149.66	(35)	139.00	(50)	144.40	(4)	150.00	144.32
1948			(27)	145.00	(60)	142.23					143.16
1949	(2)	190.00	(34)	139.41	(61)	146.47					144.89
1950	(3)	131.66	(40)	144.25	(120)	137.66	(45)	151.22			141.77
1951	(4)	167.50	(33)	143.78	(67)	163.33	(6)	163.33			144.72
1952			(80)	144.25	(281)	125.41	(56)	151.96			133.59
1953			(16)	161.25	(10)	147.00	(3)	178.33			158.10
1954			(19)	158.68	(26)	159.61			(4)	172.50	160.30
1955					(9)	163.88					163.88
1956			(23)	172.36	(31)	146.29	(50)	175.92			166.50
1957			(221)	159.54	(138)	149.02	(39)	160.89			156.03
1958	(55)	148.63	(46)	146.30	(47)	134.78	(115)	130.47	(6)	143.33	137.93
1959	(46)	146.95	(317)	129.79	(148)	129.59	(16)	146.25	(3)	138.33	131 77
1960			(75)	150.46	(71)	138.94					144.86
1961			(29)	153.62	(57)	137.45	(12)	138.33			142.34
1962			(8)	141.25	(12)	152.50					148.00
1963			(180)	134.86	(54)	133.14	(79)	139.05	(5)	133.00	135 58
1964			(35)	127.28	(143)	130.87	(238)	143.21	(59)	152.62	139.49
1965			(22)	137.72	(20)	147.00	(81)	145.50			143.69
1966	(4)	125.00	(62)	137.41	(91)	134.89	(68)	127.50			133.17
1967			(43)	135.46	(117)	127.99	(35)	132.28	(48)	147.70	133.97
1968	(5)	119.00	(68)	129 85	(103)	137.23	(82)	144.87	(36)	148.61	138.74
1969			(16)	153.75	(125)	142.36	(52)	146.92			144.52
1970			(26)	126.15	(51)	133.62	(15)	141.66			132.82
1971			(32)	152.19	(46)	132.39	(20)	154.50			143.37
1972			(22)	149.54	(12)	157.50	(16)	146.25			150.40
1973	(1)	155.00	(12)	135.00	(15)	144.33	(2)	155.00	(1)	205.00	143.71
1974	(13)	140.38	(85)	138.17	(116)	147.28	(112)	143.39	(3)	168.33	143.52
1975			(38)	146.05	(110)	149.45	(7)	155.00			148.87
1976	(2)	125.00	(61)	152.29	(59)	145.60	(54)	149.81	(17)	151.76	147.81
1977	(1)	125.00	(35)	144.71	(96)	155.94	(169)	150.74	(3)	148.33	151.58
1978	(1)	155.00	(37)	146 89	(50)	153.00	(46)	161.96	(2)	155.00	154.41
1979	(3)	158.33	(142)	138.73	(85)	139.06	(4)	152.50	(3)	178.33	139.83
1980	(2)	150.00	(63)	142.78	(32)	150.00	(8)	160.00	(3)	151.67	146.58
36-year mean	(142)	146.20	(2,112)	142.04	(2,673)	139.02	(1,496)	145.71	(197)	150.81	
	2%		32%		40%		23%		3%		
Combined mean, both clubs	(221)	142.94	(3,812)	140.02	(7,030)	136.96	(3,310)	144.56	(765)	149.58	

(3.3 pounds) heavier in September, and 0.7 kg (1.6 pounds) heavier in November.

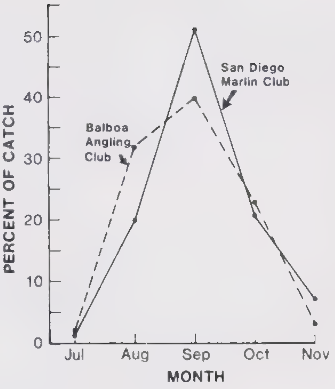

Figure 2.—Percentage of catch by month recorded for landings of striped marlin at San Diego (1960-80) and Balboa, Calif. (1945-80).

Combined mean weights for the 15,138 marlin in the sample (Table 1) show a slight decrease in mean weight to 62.1 kg (136.9 pounds) during September, the month with the highest catch, when compared with weights for August and October. In October and November mean weight increased to 65.8 kg (145 pounds) and 68 kg (150 pounds), weights that are slightly above the weight observed at the beginning of the season.

Although the mean weight of marlin taken in recent years is only slightly higher than those weights recorded in the late 1940's, there occurred a period from 1953 through 1957 when anomalous weights were observed. In 1952 the average weight recorded at the Balboa Angling Club was 60.0 kg (134 pounds) with a catch of 417 fish, a catch which was well above the average landing of 184 marlin. In 1953 the catch was low (29 marlin) but the average weight increased 10.9 kg (24 pounds) to 71.7 kg (158 pounds) over the previous year (1952). The average weight continued to be well above the long-term average (64.4 kg or 142 pounds) during the next four seasons, 1954-57, with catches of 49, 9, 103, and 398 marlin respectively. In 1956 the average weight was the maximum recorded, 75.8 kg (167 pounds). Average weights decreased in 1958 to near the long-term average but with an above average catch of 269 mar-

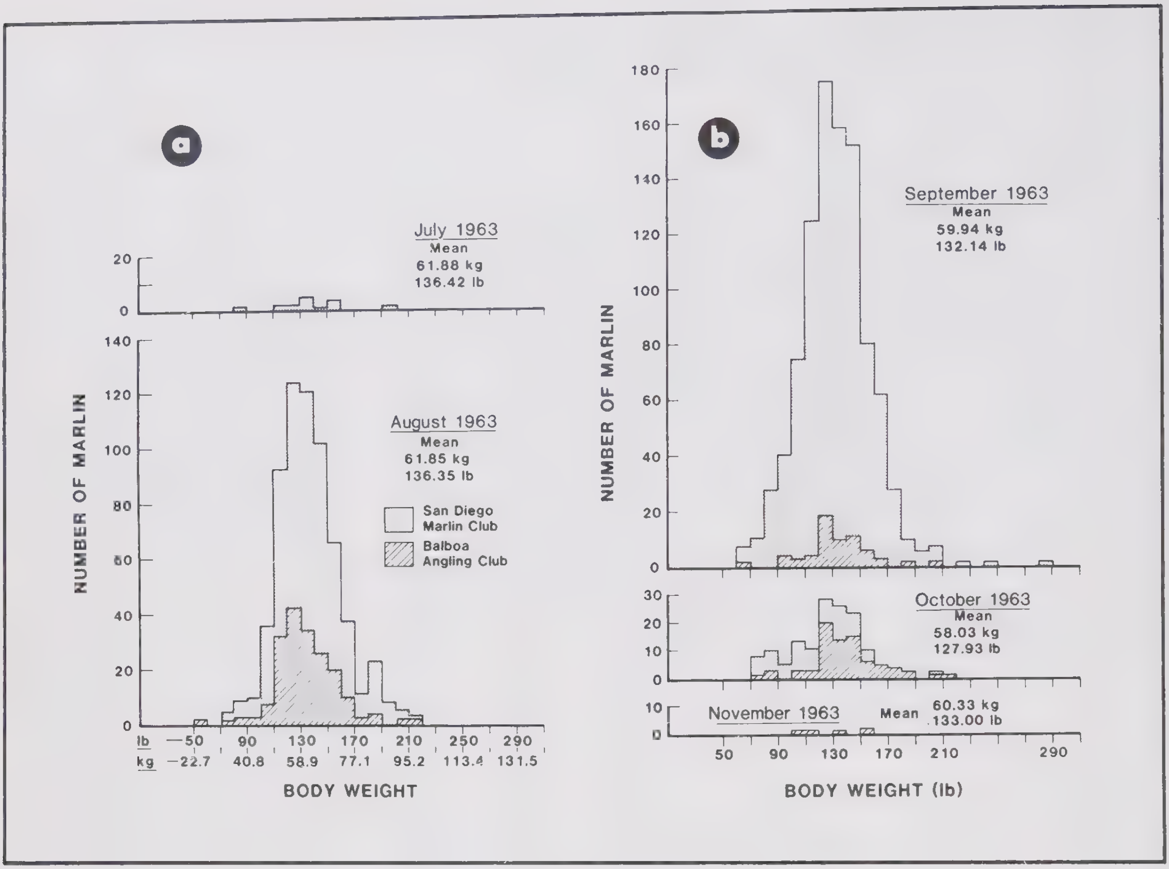

Figure 3.—Distribution of landing weights by 4.5 kg (10-pound) increments for the 1963 season.

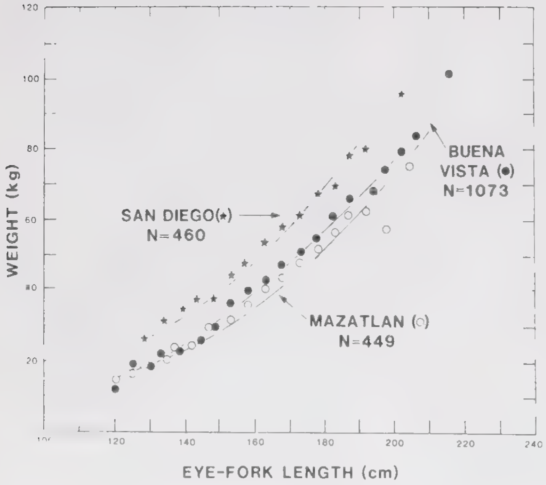

Figure 4.—Weight as a function of eye-fork length of striped marlin from the northeastern Pacific. (Buena Vista is located in the east side of the Baja California Mexico peninsula near the southern tip.) From Wares and Sakagawa (1974).

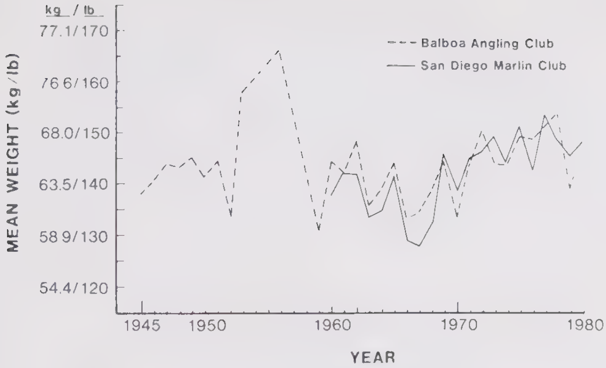

Figure 5.—Mean weight of striped marlin by year for landings at the Balboa Angling Club, 1945-1980 and the San Diego Marlin Club, 1960-1980.

lin. Data indicate that predominantly larger (older) marlin were common to the fishing area in the 5-year period from 1953-57, with marlin of lower mean weight recruited back into the fishery in 1958. From 1958 through 1980 both sets of data (Fig. 5) show no substantial change in average weight even though large catches of striped marlin have been made by the commercial longline fleet in the northeast Pacific.

Acknowledgments

The work of Karen Blakney in reviewing and tabulating recordbook data and preparing length frequency graphics for analysis is appreciated. The manuscript was reviewed by Norman Bartoo and Earl Weber and their suggestions are appreciated.

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Results of a Tagging Program to Determine Migration Rates and Patterns for Black Marlin, *Makaira indica*, in the Southwest Pacific Ocean

JAMES L. SQUIRE, JR.[1] and DAPHNE V. NIELSEN[2]

ABSTRACT

Marine game fish anglers reported tagging a total of 2,576 black marlin, *Makaira indica*, from 1968 through 1978 near the Great Barrier Reef, north Queensland, Australia, as part of the National Marine Fisheries Service Cooperative Marine Game Fish Tagging Program—Pacific Area. Sixty tagged black marlin were recaptured during an 11-year period for a recapture rate of 2.3%. Average weight of black marlin tagged was estimated to be 175 kg (385 lb). Anglers tend to overestimate weight at time of tagging and short-term recaptures (0-60 days) indicate an average angler overestimate of 16 kg (35 lb) per marlin.

Sex was determined for 28 recaptures; 25 (89%) were reported as males and 3 (11%) reported as females. Average weight of males at recapture was 91 kg (195 lb), for females, 221 kg (488 lb).

Vector analysis of time, distance, and direction data for tag recovery locations indicated migration direction (vector mean bearing) and distance (vector mean distance from point of tagging) by periods of release time: 0-60 days, 121°/72 nmi, 61-120 days, 134°/446 nmi, 121-240 days, 097°/1,256 nmi.

The greatest distance (2,100 nmi) recorded from the point of tagging was for a black marlin recaptured northeast of New Zealand, 235 days after tagging. Black marlin tagged early in the north Queensland fishing season (September) tended to migrate away from the area of tagging at a lower rate for the first 0-60 day period than black marlin tagged in October, November, or later in the fishing season.

Tag recoveries were made near the tagging location 1, 2, and 4 years after tagging. Locations of recapture for these black marlin were calculated to be a vector mean distance of 58.3 nmi from the point of tagging. Longline high catch rate areas for black marlin indicate a monthly movement for the first 240 days of release time not unlike that observed by tagging. In the summer the centers of high catch rate show a south to southeast movement off the east coast of Australia from the tagging area, then a northward movement in the winter and spring to the New Guinea-Bismark Archipelago-Solomon Islands area. The amount of interchange with the Indo-Pacific and areas to the north is unclear, although emigration from the tagging area to north of New Guinea was recorded.

INTRODUCTION

Little is known about the migratory patterns for oceanic pelagic species such as tunas and billfish in the Pacific Ocean. Only a few species of tuna, such as yellowfin tuna, *Thunnus albacares*; albacore, *Thunnus alalunga*; bluefin tuna, *Thunnus thynnus*; and skipjack tuna, *Euthynnus pelamis*, have been tagged in sufficient numbers, usually by commercial methods (trolling, live-bait, or purse seining), to determine patterns and rates of migration. Billfish have a high economic value to the commercial longline fishery but are not caught at any one time in large numbers like the tunas. Therefore, the opportunity to tag and release these fishes is more limited.

The concept of using anglers to tag and release billfish, tunas, and other pelagic marine game species, was first developed by Frank J. Mather III of the Woods Hole Oceanographic Institution, Woods Hole, Mass. (WHOI). The "Cooperative Marine Game Fish Tagging Program" was first established by WHOI with a grant from the National Science Foundation for studies in the Atlantic Ocean. Since marine anglers frequently travel worldwide to fish for billfish, some tags issued for studies in the Atlantic were being used in the Pacific starting in 1954 to tag black marlin, *Makaira indica*, blue marlin, *Makaira nigricans*, striped marlin, *Tetrapturus audax*, sailfish, *Istiophorus platypterus*, shortbill spearfish, *Tetrapturus angustirostris*, and swordfish, *Xiphias gladius*. In 1961, the senior author made a cooperative agreement with Mather to support Pacific area tagging on behalf of the U.S. Fish and Wildlife Service, Pacific Marine Game Fish Research Center/Tiburon Marine Laboratory, Tiburon, Calif., later to become a laboratory of the National Marine Fisheries Service (NMFS). The Service then assumed responsibility for the Pacific program and has continued since that time to support the tagging efforts of marine game fish anglers for billfish and other pelagic game fish species.

The tagging results discussed in this paper are for tags furnished through 1978 by the NMFS and the WHOI. Beginning in 1976, increasing numbers of black marlin have been tagged with tags furnished by New South Wales State Fisheries, Sydney, Australia, and this agency has now assumed the primary role in support of the tagging program for black marlin off north Queensland, Australia. These records are not included in the analysis portion of this paper, with the exception that data for four recoveries (6.3% of the tag recoveries reported upon) of New South Wales State Fisheries (NSWF) tags have been used in the computation of mean vector bearing and distances, sex ratios, and estimated weight data.

TAGGING AND RECOVERY

The tagging data base of this study is that portion of the black marlin catch tagged and released by anglers off the northeast coast of Australia adjacent to the Great Barrier Reef, between lat.

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[1] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

[2] Cairns Game Fishing Club, Cairns, Queensland, 4870, Australia.

14° and 18°S. The major source for recoveries is the Pacific-wide Japanese and Korean commercial longline fishery catch, and, to a minor extent, the catch of Australian and New Zealand commercial and recreational fisheries. Few recoveries could be expected from the billfish recreational fishery since the numbers of billfish taken are small compared with the catch of the commercial longline fishery (avg. 9,100 fish, 1969-78, Japanese longline data). The recreational fishery operates in a relatively restricted seasonal and geographical area near the edge of the Great Barrier Reef where the resource is available and catchable, and high rod-and-reel catch rates can be obtained. Potential recovery areas by anglers are generally restricted to the major tagging areas. The longline fishery, however, samples over a large area of the ocean and it is possible that recoveries could be made throughout the year, sometimes at considerable distances from the location of tagging. The extensive Japanese longline fishery recovers the most tagged marlin.

Black marlin are distributed widely throughout the Pacific and Indian Oceans with some catches reported in the South Atlantic Ocean. Some of the better longline fishing areas for black marlin are in the east China Sea near Taiwan, off northwest Australia, the Arafura Sea, Sulu Sea, Celebes Sea, and the Coral Sea off northeast Australia. Of interest to this migration study is that no longline effort or catches of black marlin are reported north of Australia in the eastern Arafura Sea. Between Cape York, Australia, and Papua lies the Torres Strait, a large area having a water depth of < 20 m. This shallow area may inhibit the migration of black marlin between the Coral and Arafura Seas. The distribution of black marlin as inferred from catch rates from the Japanese longline fishery in the Pacific, Indian, and South Atlantic Oceans is given in Figure 1.

Black marlin have been an important resource to the Japanese commercial longline fishery in the western Pacific since the early 1950's. Catch levels of all fleets in the western Pacific are currently about 3,000 t (metric tons), approximately one-half the peak catch in 1957, with about 59% of the southwestern Pacific black marlin catch being taken in 1976 by Japanese longliners (FAO 1979).

While the longline fishery generally targets on the tunas, in certain areas of the Pacific they may target upon marlin, sailfish, swordfish, or both tunas and billfish. Billfish comprise about 18% of the total longline catch in the Pacific (Ueyanagi 1974). However, the ex-vessel value of some species of billfish, such as striped, blue, and black marlin, may be two or more times that of some tunas, making the fraction of billfish an important factor in determining the location of fishing effort. Black marlin appears to be a target species in the western Coral Sea near the tagging area during the spring and early summer months of September through January. The distribution of longline fishing effort and catch rates obtained in the areas to the south, west, and north of the tagging area, in months subsequent to tagging, is an important factor in evaluating tag recovery data.

METHODS AND EQUIPMENT

All black marlin tagged in the Pacific under the auspices of the Cooperative Marine Game Fish Tagging Program were caught by anglers using rod-and-reel, and were tagged and released by the angler or a member of the charter boat crew. Several types of tags were used in the 1960's, the principal type being the double barbed, all-plastic FM67 tag (Fig. 2). Other tags used in small numbers included the Type "A" tag, a metal-tipped tag similar to the "H" tag, and type "B" tag, a small, single-barbed plastic tag similar to tags currently being used for tunas (Fig. 2). Since 1970, the tag distributed has been the stainless steel dart tag ("H" type). This tag has a nylon monofilament line extending from the stainless steel barb, with a yellow polyvinyl tubing sleeve over the monofilament for printed information. Numbers and letters on the yellow polyvinyl sleeve are heat embossed in black, giving the tag's serial number and return and reward information. All tags furnished by the National Marine Fisheries Service were manufactured by the Floy Tag and Manufacturing Company, Seattle, Wash.

Each tag is attached to a postcard having the tag's serial number printed on it. After tagging a fish, the angler completes the information requested on the postcard such as tagging date,

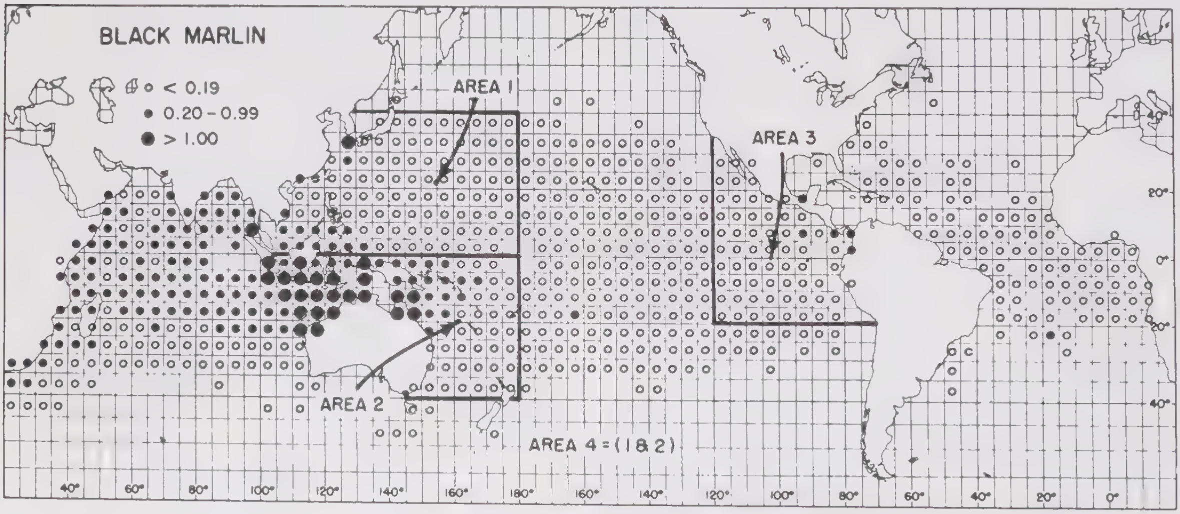


Figure 1.—Distribution of longline catch rates for black marlin in the Pacific Ocean as an indicator of resource distribution. Circles indicate mean catch rates (number of black marlin/1,000 hooks). Also shown are the boundaries of suggested black marlin stocks. From Shomura (1980).

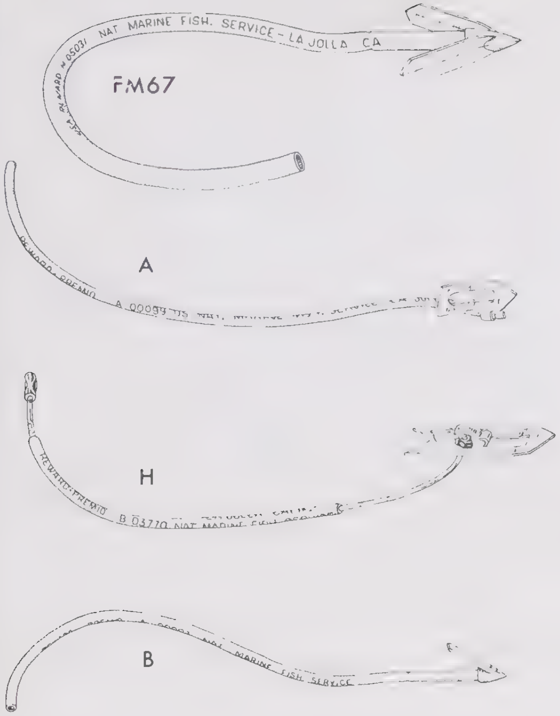


Figure 2.—Four types of dart tags used in the Pacific Ocean by the Cooperative Marine Game Fish Tagging Program.

Table 1.—Black marlin tagging off north Queensland, Australia, by year tagged and tag type, 1968-78.

Year	Number tagged	Tag types A	H	FM67	B
1968	26			26	
1969	51			51	
1970	110			110	
1971	184		127	57	
1972	288		287	1	
1973	438		378	60	
1974	337	1	335		1
1975	411	1	409		1
1976	501		501		
1977	170		170		
1978	60		60		
Total	2,576	2	2,267	305	2

location of tagging, species, estimate of fish's weight, tagger's name and address and returns it to the organization issuing the tag. Anglers who indicated a willingness to tag and release billfish were issued tagging equipment which consisted of a stainless steel applicator tip which must be mounted in a tagging pole, tags, instructions, and tagging flags for recognition of a billfish tagged and released. There was no charge for the tagging equipment.

When billfish are recovered, the recoverer receives a monetary reward upon sending in information on the tag number, species, date, and location of recovery. The recoverer sometimes adds information on water temperature at the time of recapture, length and weight measurements, sex, and gonad weight data.

RELEASE DATA

Cooperating marine game fish anglers and charter boat captains have tagged and released 2,885 black marlin in the Pacific Ocean using NMFS and WHOI tags since 1961. Of this number, 2,576 black marlin (89%) were tagged along the Great Barrier Reef off the north Queensland coast of Australia. The coordination of tagging for black marlin in this area was by the Cairns Game Fish Club, Cairns, Australia. Other locations in the Pacific where black marlin were reported to have been tagged were off the coasts of Panama and Hawaii, and near the southern tip of Baja California, Mexico.

The numbers of black marlin tagged in the north Queensland area are listed in Table 1 by year and tag type. Of the 2,576 black marlin tagged, 2,276 (88.0%) were tagged with "H" type tags and 305 (11.8%) with FM67 type tags. The remainder were tagged with "A" or "B" type tags.

Figure 3 shows the distribution of tagging effort by year and average estimated weights as given by the angler, in relation to tagging locations along the outer islands and reefs of the Great Barrier Reef. September, October, and November are the major months for tagging black marlin, with percentages of 21.6, 49.0, and 24.1, respectively. The geographical area where the most black marlin were tagged was along the Great Barrier Reef from lat. 16°00′ to 16°30′S. This area includes the reefs known as Hope, Nicholas, Onyx, Spur, Opal, St. Crispin, Linden Bank, and Agincourt Reefs No. 1 and 2. Data given in Figure 3 indicate that from 1972 to 1974 tagging effort shifted northward off the Queensland area. This was probably due to the development near the outer reefs of floating or island facilities for the angler, allowing him easier access to waters distant from Cairns, Queensland.

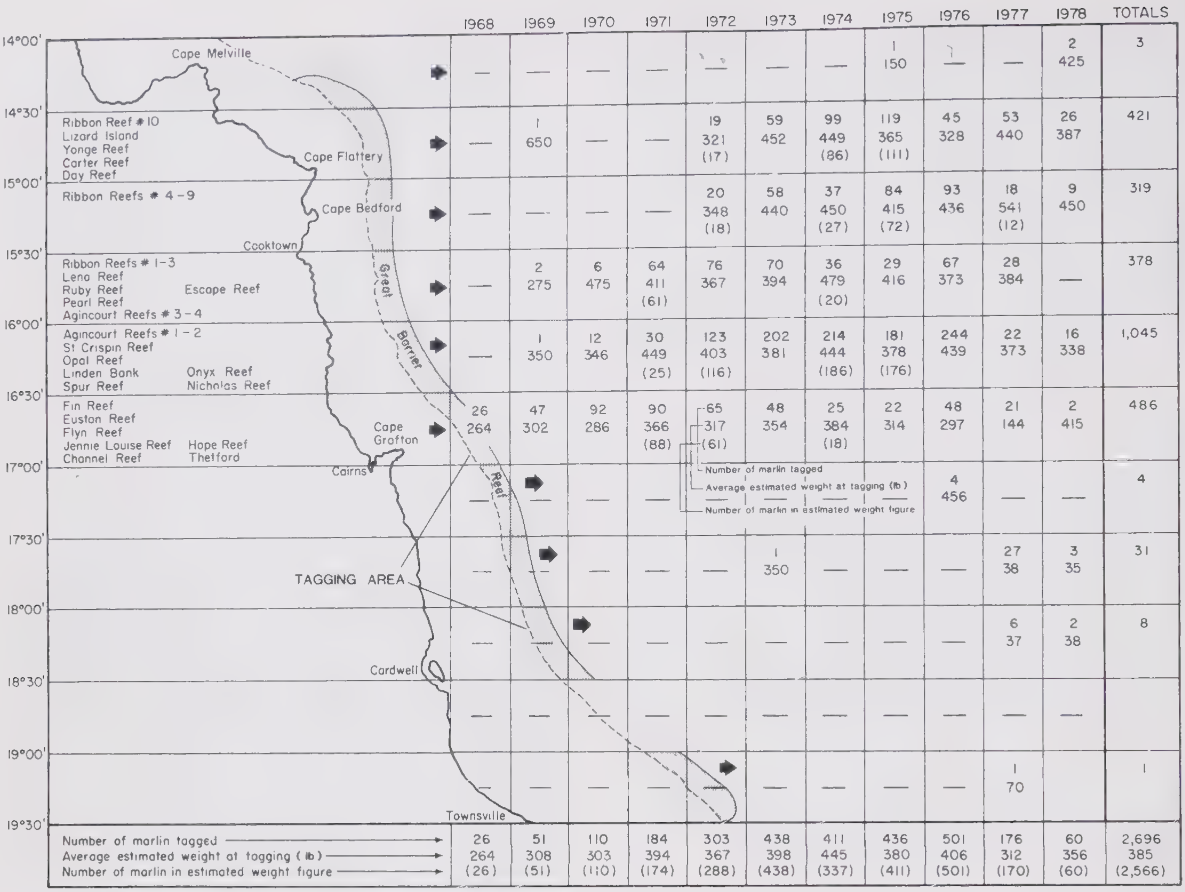
RECOVERIES

Of the 59 recaptures reported for black marlin tagged during the years 1968-78, 52 (88%) were recaptured by Japanese and Korean commercial longline fishing vessels, 4 (7%) by marine anglers, and 2 (3%) by Australian commercial fishermen (trawlers or netters); 1 (2%) was a beached marlin. Table 2 gives black marlin release, recapture, and biological data for those tagged with NMFS or WHOI tags. Data from four New South Wales State recoveries used elsewhere in the analysis are not listed in Table 2. Of the 59 returns, one return could not be matched to a tag report card.

RECOVERY RATES

A total of 2,576 black marlin was tagged off Queensland: 2,267 with the "H" type tags, 305 with the FM67, 2 with the "A" type, and 2 with the "B" type. Of these, 1.3% of the FM67 tags and 2.4% of the "H" tags were recovered, with an overall recovery rate of 2.3%. A breakdown of recovery rates for this area by year and by type of tag is given in Table 3.

Of the total of 189 black marlin reported tagged in other areas of the Pacific, 70 were tagged with FM67 type tags and 119 with "H" type tags. None has been reported recovered.



Latitude	Area	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	TOTALS
14°00'–14°30'		—	—	—	—	—	—	—	1 150	—	—	2 425	3
14°30'–15°00'	Ribbon Reef # 10 Lizard Island Yonge Reef Carter Reef Day Reef	—	1 650	—	—	19 321 (17)	59 452	99 449 (86)	119 365 (111)	45 328	53 440	26 387	421
15°00'–15°30'	Ribbon Reefs # 4 – 9	—	—	—	—	20 348 (18)	58 440	37 450 (27)	84 415 (72)	93 436	18 541 (12)	9 450	319
15°30'–16°00'	Ribbon Reefs # 1 – 3 Leno Reef Ruby Reef Pearl Reef Agincourt Reefs # 3 – 4 Escape Reef	—	2 275	6 475	64 411 (61)	76 367	70 394	36 479 (20)	29 416	67 373	28 384	—	378
16°00'–16°30'	Agincourt Reefs # 1 – 2 St Crispin Reef Opal Reef Linden Bank Spur Reef Onyx Reef Nicholas Reef	—	1 350	12 346	30 449 (25)	123 403 (116)	202 381	214 444 (186)	181 378 (176)	244 439	22 373	16 338	1,045
16°30'–17°00'	Fin Reef Euston Reef Flyn Reef Jennie Louise Reef Channel Reef Hope Reef Thetford	26 264	47 302	92 286	90 366 (88)	65 317 (61)	48 354	25 384 (18)	22 314	48 297	21 144	2 415	486
17°00'–17°30'		—	—	—	—	—	—	—	—	4 456	—	—	4
17°30'–18°00'		—	—	—	—	—	1 350	—	—	—	27 38	3 35	31
18°00'–18°30'		—	—	—	—	—	—	—	—	—	6 37	2 38	8
18°30'–19°00'		—	—	—	—	—	—	—	—	—	—	—	
19°00'–19°30'		—	—	—	—	—	—	—	—	—	1 70		1
	Number of marlin tagged Average estimated weight at tagging (lb) Number of marlin in estimated weight figure	26 264 (26)	51 308 (51)	110 303 (110)	184 394 (174)	303 367 (288)	438 398 (438)	411 445 (337)	436 380 (411)	501 406 (501)	176 312 (170)	60 356 (60)	2,696 385 (2,566)

Figure 3.—Locations of black marlin tagging immediate to the Great Barrier Reef off north Queensland, Australia, by 30° latitude areas, by year and number of black marlin tagged, and average estimated weight by anglers at time of tagging. Note—estimated weight may vary from actual weight, see text. (For conversion of pounds to kilograms, lb × 0.4536 = kg).

TAGGING AND RECOVERY WEIGHT DATA

Upon tagging a black marlin, one of the items requested from the angler was an estimate of the marlin's weight. The average weight estimated by angler at the time of tagging, for 2,566 marlin having weight data reported, was 175 kg (385 lb). Average estimated weights by year and by 30° latitude area off north Queensland are given on Figure 3. The largest recorded average weight by year was 202 kg (445 lb) in 1974. The largest number of marlin tagged, and the largest average weight of 186 kg (410 lb), occured at lat. 16°00′ to 16°30′S. This area includes Agincourt Reefs #1 and #2, Linden Bank, and St. Crispan, Opal, Spur, Onyx, and Nicholas Reefs.

Estimated tagging weight varied greatly with landing weight as seen by catches recorded at Cairns and Lizard Island weighing stations from 1 September to 31 December 1970-78 (Table 4). The average weight of black marlin from the landing records is 346 kg (762 lb). Estimates of weight at time of tagging averaged 175 kg (385 lb) or 171 kg (377 lb) less than the weights recorded at the weighing station.

The weight data on recaptured marlin were sometimes submitted with additional information on the recovery. In the case of the commercial longline fishery the weights were with the bill and a portion of the head removed at about the area of the eye orbit. The reported weight must therefore be increased by a factor of 1.1 (Ueyanagi[1]) to give the approximate "round weight" of the fish.

Fifty-one marlin had weight and/or length data accompanying information on the geographical location and time of recapture. Upon examination of the weight and length data for the recaptures, it was determined that for five marlin the data were inadequate to determine total weight. Of 46 black marlin recaptured by the commercial longline fishery, having angler estimated weight data at tagging, 30 were recaptured at total weight less than estimated by the angler, 15 at weights greater than estimated, and 1 at the same weight. The average angler overestimate of black marlin recaptured at tagging, when compared with the recapture

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[1] Shoji Ueyanagi, Far Seas Fisheries Research Laboratory, Japan Fisheries Agency, 1000 Orido, Shimizu, 424, Japan, pers. commun.

Table 2.—Black marlin release and recapture data, 1968-1978. Angler's Country - (U.S.) United States, (NZ) New Zealand, (A) Australia. Others as given.

Releases				Recaptures					Biological data			
Year	Date (SWFC No.)	Location	Tagger/Captain	Date	Location	Recovered by	Distance from point of tagging	Days at large	Estimated weight at release	Weight at recapture	Length	Sex
1968	3 Oct. (74)	Euston Reef	Mrs. B. Dyer/(A) C. Chambers	Jan. 1969	Narlinga Beach 20 mi. S. of Innisfail, Aust.	J. Giddins Innisfail, Aust.	55	95 (est.)	----	----	----	-
1969	2 Nov. (102)	Hope Reef	Bob Dyer/(A) C. Chambers	Oct. 1970	Lat. 15°30'S Long. 145°55'E	Kompira maru No. 28 (Japan)	60 N	364	84 kg (158 lbs)	60 kg[1] (132 lbs)	----	-
1971	11 Oct. (120)	Escape Reef	P. Van Vleck/(U.S.) P. Bristow	Apr. 17, 1972	Lat. 03°33'S Long. 166°03'E	Jinam No. 26 (Korea)	1,440 NE	180	23 kg (50 lbs)	42 kg[1] (92 lbs)	104.6 cm[2]	-
1972	31 Aug. (134)	Hope Reef	H. Henze/(U.S.) P. Bristow	Oct. 31, 1972	Lat. 15°42'S Long. 146°06'E	Tsurugi maru (Japan)	50 E	61	91 kg (200 lbs)	----	173.0 cm[2]	M
1972	10 Oct.) (135)	Linden Bank	V. Price/(U.S.) T. Curran	Nov. 10, 1972	Lat. 16°00'S Long. 146°00'E	Kompira maru No. 28 (Japan)	17 N	31	136 kg (300 lbs)	30 kg (68 lbs)	----	-
1970	13 Oct. (136)	Off Cairns, Aust.	P. Gay/(A) D. wallace	Nov. 17, 1971	Lat. 15°30'S Long. 146°15'E	Kompira maru No. 28 (Japan)	83 NW	400	----	70 kg (154 lbs)	----	-
1972	10 Oct. (140)	Off Cairns, Aust.	D. Lyall/(A) K. Lyall	Nov. 10, 1972	Lat. 18°32'S Long. 148°36'E	Genyō maru (Japan)	145 SE	31	91 kg (200 lbs)	43 kg (95 lbs)	157 cm[2]	M
1972	11 Sept. (141)	Near Ribbon Reefs	C. Simms/(U.S.) P. Bristow	Oct. 18, 1972	Lat. 14°45'S Long. 145°55'E	Seiho maru No. 58 (Japan)	15 N	37	68 kg (150 lbs)	68 kg (Est 150 lbs)	----	-
1972	25 Sept. (142)	Opal Reef	R. Schubot/(U.S.) D. Wallace	Nov. 22, 1972	Lat. 16°00'S Long. 146°12'E	Seiwa maru (Japan)	22 NE	58	68 kg (150 lbs)	----	172 cm[2]	M
1972	19 Oct. (144)	Agincourt Reef	G. Bos/(U.S.) P. Wright	Mar. 9, 1973	Lat. 03°00'S Long. 144°00'E	Fuku maru No. 11 (Japan)	1,080 N	141	273 kg (600 lbs)	280 kg (616 lbs)	----	-
1973	3 Oct. (160)	Ruby Reef	J. Del Guericio/(U.S.) P. Bristow	Oct. 22, 1973	Lat. 18°09'S Long. 148°03'E	Genyō maru (Japan)	197 SE	19	91 kg (200 lbs)	62 kg (136 lbs)	175 cm	M
1973	6 Oct. (162)	Lena Reef	J. Del Guercio/(U.S) P. Bristow	Nov. 11, 1973	Lat. 15°28'S Long. 145°59'E	Satsuma Seium maru No. 2 (Japan)	13 NE	35	91 kg (200 lbs)	----	191 cm[2]	-
1973	11 Oct. (163A)	Agincourt Reef	R. Vincent/(A) V. Vlassof	Nov. 1, 1973	Lat. 16°07'S Long. 146°16'E	Fukushime maru (Japan)	33 SE	21	182 kg (400 lbs)	84 kg (185 lbs)	192 cm[2]	M
1973	4 Oct. (174)	Off Cairns	----	Nov. 12, 1973	Lat. 15°05'S Long. 146°10'E	Haybusa maru No. 3 (Japan)	90 N (est.)	39 (est.)	----	Est 50 kg (110 lbs)	Est 2 m	-
1974	10 Oct. (176)	Opal Reef	J. Gay/(A) D. Wallace	Nov. 24, 1974	Lat. 14°26'S Long. 145°44'E	Yakushi maru No. 38 (Japan)	120 N	35	68 kg (150 lbs)	63 kg (139 lbs)	235 cm	-
1973	5 Nov. (177)	Agincourt Reef #2	E. Gould/(U.S.) P. Bristow	Nov. 4, 1974	Lat. 17°23'S Long. 147°05'E	Kana maru (Japan)	110 SE	364	182 kg (400 lbs)	88 kg[1] (194 lbs)	192 cm[2]	M 1,400 g[3]

Table 2.—Continued.

Releases				Recaptures					Biological data			
Year	Date (SWFC No.)	Location	Tagger/Captain	Date	Location	Recovered by	Distance from point of tagging	Days at large	Estimated weight at release	Weight at recapture	Length	Sex
1974	4 Nov. (178)	Linden Bank	T. Evans/(A) V. Vlassof	Nov. 16, 1974	Lat. 17°11'S Long. 147°99'E	*Kana maru* (Japan)	85 SE	12	91 kg (200 lbs)	98 kg (216 lbs)	193 cm[2]	M 2,100 g[3]
1974	12 Sept. (179)	Linden Bank	M. Florence/(A) L. Woodbridge	Nov. 6, 1974	Lat. 13°55'S Long. 145°11'E	*Genyō maru* (Japan)	150 N	55	----	82 kg[1] (180 lbs)	197 cm[2]	M
1973	8 Oct. (180)	No. 10 Ribbon Reef	J. Del Guercio/(U.S.) P. Bristow	Oct. 8, 1974	Lat. 16°01'S Long. 146°42'E	*Ashyu maru* (Japan)	95 SE	364	136 kg (300 lbs)	94 kg[1] (185 lbs)	184 cm[2]	M
1974	5 Oct. (181)	Onyx Reef	H. Nordaas/(U.S.) K. Klaproth	Oct. 26, 1974	Lat. 15°01'S Long. 145°57'E	*Ashyu maru* (Japan)	63 N	21	----	64 kg[1] (141 lbs)	180 cm[2]	M
1974	4 Oct. (182)	No. 9 Ribbon Reef	F. Inscho/(U.S.) P. Wright	Oct. 28, 1974	Lat. 13°40'S Long. 145°45'E	*Wakatori maru* (Japan)	72 N	24	68 kg (150 lbs)	60 kg (132 lbs)	174 cm[2]	-
1974	25 Sept. (183)	Agincourt Reef	H. Nordass/(U.S.) K. Klaproth	Dec. 26, 1974	Lat. 33°45'S Long. 151°22'E	N. Thompson near Long Reef, Sydney, Aust.	1,290 S	92	136 kg (300 lbs)	77 kg (169 lbs)	----	-
1974	14 Sept. (184)	No. 10 Ribbon Reef	S. Zuckerman/U.S.) P. Bristow	Nov. 18, 1974	Lat. 18°45'S Long. 150°10'E	*Genyō maru* (Japan)	351 SE	65	----	116 kg[1] (255 lbs)	206 cm[2]	M
1973	2 Sept. (185)	No. 2 Ribbon Reef	R. Meyer/(A) P. Bristow	Oct. 6, 1973	Lat. 16°18'S Long. 146°30'E	*Funakawa maru* (Japan)	70 SE	34	136 kg (300 lbs)	----	170 cm.	
1974	8 Oct. (203)	No. 10 Ribbon Reef	D. Phipps/(U.S.) L. Woodbridge	Nov. 7, 1974	Lat. 22°27'S Long. 154°32'E	Longliner (name unknown, Japan)	670 SE	30	45 kg (100 lbs)	52 kg (114 lbs)	----	
1972	13 Sept. (204)	Off Cairns	M. Johnson (U.S.) D. Wallace	Apr. 30, 1975	Elizabeth Reef near Tutakakz, New Zealand	R. Dazeley/(-) S. Pritchard, Capt.	1,875 SE	959	159 kg (350 lbs)	147 kg (325 lbs)	108 cm[4]	-
1974	14 Sept. (205)	No. 6 Ribbon Reef	B. May/(U.S.) D. Wallace	Oct. 13, 1974	Lat. 15°30'S Long. 146°10'E	*Etsuzan maru* (Japan)	32 SE	29	114 kg (250 lbs)	60 kg[1] (132 lbs)	170 cm[2]	M
1973	19 Sept. (206)	Escape Reef	G. Matthews/(U.S.) P. Bristow	Oct. 28, 1974	Lat. 16°30'S Long. 146°45'E	*Etsuzan maru* (Japan)	60 SE	404	91 kg (250 lbs)	73 kg[1] (161 lbs)	184 cm[2]	M 650 g[3]
1974	2 Oct. (207)	No. 10 Ribbon Reef	R. Schubot/(U.S.) D. Wallace	Feb. 24, 1975	Lat. 31°03'S Long. 153°04'E near Korogora Pt. north of Sidney, Aust.	V. Jordan Hat Head, NSW, Aust.	1,200 S	145	114 kg (250 lbs)	76.2 kg (168 lbs)	2.58 m	-
1974	17 Oct. (208)	Thetford Reef	R. Griffin/(N.Z.) J. Crump	Jun. 9, 1975	Lat. 34°03'S Long. 175°56'W	*Lein Ho No. 1* (Korea)	2,100 SE	235	36 kg (80 lbs)	45 kg (100 lbs)	----	F
1976	22 Sept. (219)	No. 10 Ribbon Reef	R. Schubot/(U.S.) D. Wallace	Oct. 15, 1976	No. 5 Ribbon Reef	E. Palmar, Angler P. Wright, Capt.	30 S	23	148 kg (325 lbs)	----	----	-

Table 2.—Continued.

Releases				Recaptures					Biological data			
Year	Date (SWFC No.)	Location	Tagger/Captain	Date	Location	Recovered by	Distance from point of tagging	Days at large	Estimated weight at release	Weight at recapture	Length	Sex
1975	5 Oct. (220)	No. 10 Ribbon Reef	J. Del Guerico/(U.S.) P. Bristow	Oct. 10, 1976	Linden Band	M. Mather, Angler G. Mills, Capt.	87 S	370	136 kg (300 lbs)	Est 68 kg (150 lbs)	----	-
1974	10 Oct. (227)	Carter Reef	O. Phipps/(U.S.) L. Woodbridge	Nov. 10, 1974	Lat. 14°33'S Long. 145°48'E	Yakushi maru (Japan)	6 E	41	----	340 kg (749 lbs)	410 cm	-
1975	14 Sept. (228)	No. 10 Ribbon Reef	M. Cohn/(U.S.) P. Bristow	Oct. 8, 1975	Lat. 16°01'S Long. 146°16'E	Oyama maru (Japan)	78 S	24	68 kg (150 lbs)	----	177 cm	-
1975	13 Sept. (231)	No. 3 Ribbon Reef	I. Marr/(A) D. Hayes	Nov. 1, 1975	Lat. 17°12'S Long. 147 °02'E	Kaiei maru (Japan)	25 SE	49	114 kg (250 lbs)	89 kg (196 lbs)	----	-
1975	9 Oct. (233)	Jenny Louise	K. Klaproth/(A) M. Klaproth	Feb 6, 1976	Off Inyadde Pt. South of Jervis NSW Aust.	T & C Puglisi Ulladulla, NSW Aust.	1,320 S	120	114 kg (250 lbs)	67 kg (148 lbs)	2,660 mm^{5} 2,380 mm^{6}	-
1974	14 Nov. (234)	Linden Bank	D. Roux/(S. Africa) P. Wright	Oct. 20, 1975	Lat. 14°46'S Long. 146°03'E	Oyama maru (Japan)	100 N	349	176 kg (80 lbs)	----	163 cm	-
1974	18 Sept. (235)	No. 10 Ribbon Reef	F. Rice/(U.S.) D. Wallace	Oct. 31, 1975	Lat. --°13'S Long. 144°50'E	Oyama maru (Japan)	95 NW	408	125 kg (275 lbs)	----	184 cm	-
1974	27 Sept. (236)	Agincourt Reef	P. Furnell/(A) G. White	Dec. 5, 1975	Lat. 21°30'S Long. 155°19'E	Sagami maru (Japan)	665 SE	434	91 kg (200 lbs)	----	191 cm	F 1,100 g^{3}
1975	6 Sept. (237)	No. 10 Ribbon Reef	D. Etheridge/(-) P. Wright	Oct. 12, 1976	Lat. 17°58'S Long. 147°30'E	Etsuzan maru (Japan)	220 SE	402	114 kg (250 lbs)	89 kg (196 lbs)	188 cm^{2}	M
1975	30 Oct. (238)	No. 10 Ribbon Reef	E. Gould/(U.S.) G. Hallam	Oct. 31, 1976	Lat. 13°44'S Long. 144°44'E	Etsuzan maru (Japan)	90 NW	367	91 kg (200 lbs)	82 kg (180 lbs)	186 cm^{2}	M
1974	11 Nov. (239)	Opal Reef	S. Lindsay, Jr./(U.S.) K. Klaproth	Nov. 31 1976	Lat. 13°38'S Long. 145°02'E	Etsuzan maru (Japan)	162 NW	733	136 kg (300 lbs)	82 kg (180 lbs)	185 cm^{2}	M
1975	9 Oct. (240)	No. 10 Ribbon Reef	J. Del Guerico/(U.S.) P. Bristow	Nov. 10, 1976	Lat. 14°05'S Long. 145°21'E	Etsuzan maru (Japan)	49 NW	397	136 kg (300 lbs)	64 kg (141 lbs)	174 cm^{2}	M 3,020 g^{3}
1974	18 Nov. (241)	Opal Reef	H. Samuels/(A) D. Wallace	Nov. 10, 1976	Lat. 14°05'S Long. 145°21'E	Etsuzan maru (Japan)	126 NW	723	114 kg (250 lbs)	64 kg (141 lbs)	174 cm^{2}	M 1,200 g^{3}
1976	11 Nov. (242)	Linden Bank	A. Virsakis/(-) D. Wallace	Dec. 20, 1976	Lat. 20°00'S Long. 153°44'E	Sagami maru (Japan)	500 SE	45	91 kg (200 lbs)	----	177 cm	-
1976	21 Sept. (243)	No. 9 Ribbon Reef	H. Breyer/(U.S.) P. Bristow	Nov. 28, 1976	Lat. 16°50'S Long. 147°05'E	Kompira maru No. 8 (Japan)	138 SE	68	114 kg (250 lbs)	80 kg (176 lbs)	236 cm (TL,)	-
1975	26 Nov. (244)	Euston Reef	P. Whelan/(A) B. Apnich	Nov. 6, 1975	Lat. 13°58'S Long. 145°03'E	Kaiyo maru (Japan)	180 NE	346	102 kg (225 lbs)	87 kg (191 lbs)	188 cm^{2}	M 2,500 g^{3}

Table 2.— Continued.

Releases				Recaptures					Biological data			
Year	Date (SWFC No.)	Location	Tagger/Captain	Date	Location	Recovered by	Distance from point of tagging	Days at large	Estimated weight at release	Weight at recapture	Length	Sex
1976	4 Nov. (245)	Opal Reef	J. Pilkington/(A) N. Jackson	Nov. 7, 1976	Lat. 15°38'S Long. 146°10'E	Yakusi maru No. 38 (Japan)	36 NE	3	227 kg (500 lbs)	65 kg (143 lbs)	215 cm	
1976	15 Sept. (246)	No. 7 Ribbon Reef	D. Sheperdson/(A) P. Wright	Nov. 10, 1976	Lat. 16°37'S Long. 146°40'E	Yakushi maru No. 38 (Japan)	98 SE	56	112 kg (247 lbs)	95 kg (209 lbs)	305 cm	-
1976	22 Oct. (255)	No. 3 Ribbon Reef	C. Phipps/(U.S.) L. Woodbridge	Dec. 9, 1977	Lat. 18°35'S Long. 148°07'E	Kompira maru No. 8 (Japan)	200 SE	413	91 kg (200 lbs)	----	----	-
1976	6 Dec. (256)	Linden Bank	H. Nordass/(U.S.) K. Klaproth	Oct. 16, 1977	Lat. 15°35'S Long 146°04'E	Kompira maru No. 8 (Japan)	38 NW	416	----	102 kg (224 lbs)	275 cm	-
--	Tag #18030 (257)	----	----	Oct. 23, 1977	Lat. 16°05'S Long. 146°40'E	Aomori maru	----	----	----	138 kg[1] (304 lbs)	220 cm	M
1976	15 Oct. (258)	Opal Reef	R. Mulholland/(-) D. Hayes	Oct. 17, 1977	Lat. 16°03'S Long. 146°13'E	Funakawa maru (Japan)	18 NE	367	91 kg (200 lbs)	----	183 cm	M
1976	28 Sept. (259)	No. 2 Ribbon Reef	D. Schubot/(U.S.) D. Wallace	Nov. 5, 1977	Lat. 15°35'S Long. 146°18'E	Ashu maru (Japan)	32 NE	327	80 kg (175 lbs)	72 kg[1] (158 lbs)	178 cm	M
1975	7 Nov. (260)	Opal Reef	P. Marvin/(U.S.) D. Wallace	Nov. 24, 1977	Lat. 17°43'S Long. 147°26'E	Fukuyoshi maru No. 25 (Japan)	128 SE	747	91 kg (200 lbs)	Est 75 kg (165 lbs)	----	-
1973	29 Oct. (261)	No. 10 Ribbon Reef	E. Gould/(U.S.) P. Bristow	Oct. 22, 1977	Lat. 14°21'S Long. 145°46'E	Oyama maru (Japan)	25 N	1,453	136 kg (300 lbs)	----	205 cm	M
1977	20 Sept. (269)	No. 1 Ribbon Reef	R. Estrada/(Ecuador) P. Bristow	Oct. 9, 1977	Lat. 15°28'S Long. 146°05'E	Fukuichi maru (Japan)	20 NW	19	68 kg (150 lbs)	60 kg (132 lbs)	205 cm	-
1976	3 Oct. (281)	No. 5 Ribbon Reef	A. Remley/(A) G. Hallam	Oct. 31, 1978	Lat. 16°31'S Long. 146°50'E	Yakushi maru No. 7 (Japan)	90 SE	758	250 kg (550 lbs)	115 kg (253 lbs)	2.5 m	-
1977	29 Sept. (282)	Linden Bank	C. Edwards/(A) W. Edwards	Nov. 6 , 1978	Lat. 17°00'S Long. 147°30'E	Yakushi maru No. 7 (Japan)	91 SE	403	136 kg (300 lbs)	120 kg (264 lbs)	2.5 m	-

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[1] Gilled and gutted.
[2] Eye orbit (posterior) to fork.
[3] Gonad weight.
[4] Fork to anterior portion of jaw (lower)
[5] Bill tip to fork.
[6] Lower jaw tip to fork.

Table 3.—Tag return rates by year and tag type for black marlin tagged off north Queensland, Australia, as part of the Cooperative Marine Game Fish Tagging Program—Pacific Area (NMFS/WHOI). (For tagging 1968-78.) Total tag recovery rate (%): FM67 305T/4R = 1.3%; H 2,267T/56R = 2.4% (1 H tag recovered, tagging date unknown); no recoveries for either A or B tags.

Year	Type	No. tagged	No. recovered	Recovery rate (%)
1968	FM67	26	1	3.8
	H	0		
	A	0		
	B	0		
1969	FM67	51	1	1.9
	H	0		
	A	0		
	B	0		
1970	FM67	110	1	0.9
	H	0		
	A	0		
	B	0		
1971	FM67	57	1	1.7
	H	127	1	0.8
	A	0		
	B	0		
1972	FM67	1	0	0.0
	H	287	7	2.4
	A	0		
	B	0		
1973	FM67	60	0	0.0
	H	378	9	2.4
	A	0		
	B	0		
1974	FM67	0		
	H	335	17	5.1
	A	1	0	0.0
	B	1	0	0.0
1975	FM67	0		
	H	409	9	2.2
	A	1	0	0.0
	B	1	0	0.0
1976	FM67	0		
	H	501	10	2.0
	A	0		
	B	0		
1977	FM67	0		
	H	170	2	1.2
	A	0		
	B	0		
1978	FM67	0		
	H	60	0	0.0
	A	0		
	B	0		
		2,576	59	

Table 4.—Black marlin weights as recorded by year, 1 September through 31 December 1970-78, at Cairns and Lizard Island, Queensland, Australia.

Year	Number marlin	Total weight kg	Total weight lb	Average kg	Average lb	Heaviest kg	Heaviest lb	Lightest kg	Lightest lb
1970	47	12,271	27,053	261	575	558	1,231	35	77
1971	69	21,078	46,468	305	673	514	1,133	40	89
1972	107	34,177	75,346	319	704	576	1,271	78	172
1973	134	46,000	101,411	343	756	654	1,442	20	45
1974	64	22,775	50,210	356	784	535	1,180	98	215
1975	78	28,023	61,778	359	792	620	1,367	99	218
1976	59	22,043	48,596	373	823	583	1,286	84	186
1977	49	21,273	46,899	434	957	600	1,323	110	243
1978	37	15,036	33,149	406	896	616	1,358	118	261
Total	644	222,676	490,910						
	346 kg (762 lb) average								

weight for a release time of 0-60 d, was 16 kg (35 lb). For recaptures made 61-120 d after release, the average angler overestimate at tagging was 21 kg (46 lb). Estimated weights at tagging and recapture were compared within release time periods, and the results listed in Table 5. These calculations assume no growth, therefore an increase in recapture weight vs. weight at tagging would be expected as time progressed. However, the average recaptured weight decreased when compared with estimated weight at tagging during periods 0-60 and 61-120 d after release.

Table 5.—Average weights of black marlin as estimated by the angler at time of tagging and compared with weights reported upon recovery: estimated tagging weight vs. recorded weights by time periods.

Period	No. of fish	Average weight kg	Average weight lb
0-60 d	16	[1] + 20.6	[1] + 45.5
61-120 d	4	[1] + 41.9	[1] + 92.5
121-240 d	5	[2] − 2.7	[2] − 6.0
241-365 d	7	[2] − 3.8	[2] − 8.4
366d-2 yr	9	[1] + 19.5	[1] + 43.0
2-3 yr	3	[1] + 14.3	[1] + 31.6
3-4 yr	1	[1] + 36.2	[2] 80.0

Overestimate (+), fish recovered at weights < reported tagged.

[2] Underestimate (-), fish recovered at weights > reported tagged.

SEX RATIO OF RECAPTURED MARLIN

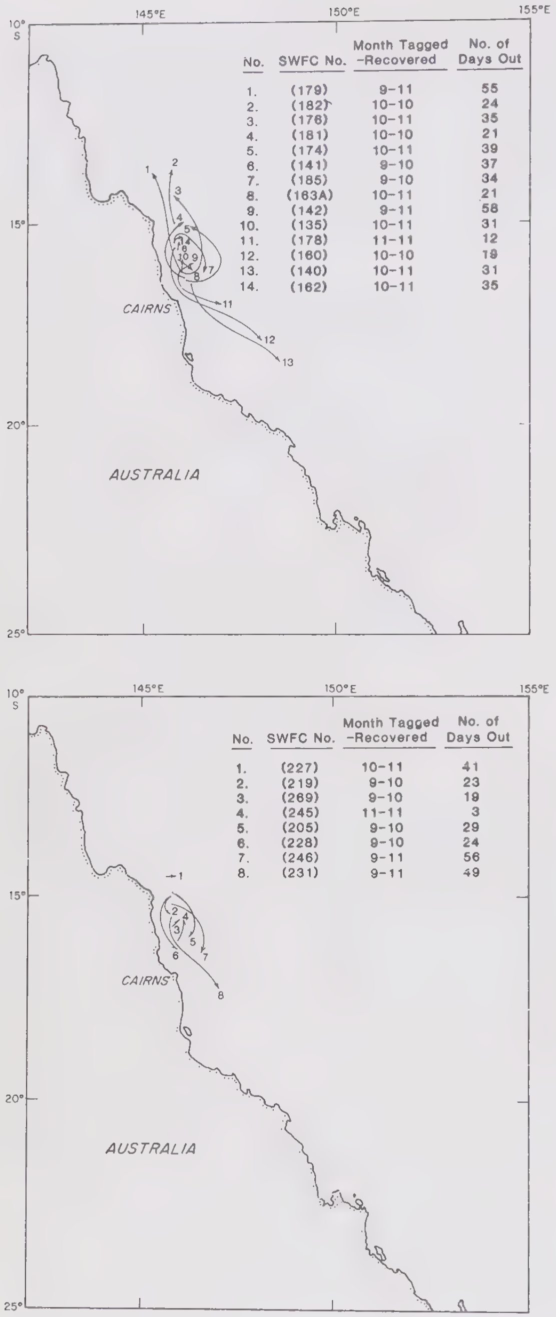
Some longline vessel crews recorded the sex of tagged black marlin upon recapture. One angler also gave this information on a recaptured marlin. Sex information was given for 28 recoveries including two recaptures from black marlin tagged with NSWF tags, and of this number, 25 (89%) were reported as males and 3 (11%) as females. The average weight of the 25 males recovered was 91 kg (193 lb), and 221 kg (449 lb) for the three females. The average weight for the small sample of females recovered was determined from black marlin weighing 45 kg (100 lb), 95 kg (209 lb), and 479 kg (1,056 lb).

MIGRATORY PATTERNS AND RATES

Black marlin occur throughout the Pacific Ocean between about lat. 40°N and 45°S, but their population density, as measured by the Japanese longline catch rate data, is low except in certain geographical areas. The stock structure of black marlin is not fully understood. Isolated high catch-rate areas are observed in the western and eastern Pacific. It has been suggested that two stocks (eastern/western) or three stocks (eastern/northwestern/northeastern) may be present (Shomura 1980). There is a strong possibility of mixing between black marlin stocks in the Indian Ocean, Indo-Pacific, and the western Pacific.

Figures 4-8 show plots of black marlin tag and recovery locations, grouped by release time periods. All recoveries >500 nmi from the tagging location off the Great Barrier Reef, Queensland, Australia, regardless of release time period, are shown in Figure 9. Information on recovery number, month of tagging, and number of days from release to recovery are included in these figures and lines connecting the tagging and recapture points do not indicate the exact migratory path of the tagged fish.

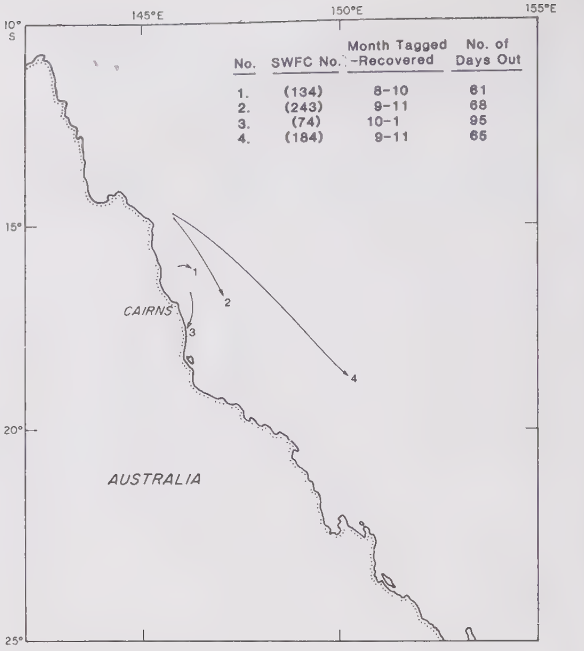
When these recovery distances over time (as measured by days from release to recapture) are presented, it can be seen that



No.	SWFC No.	Month Tagged -Recovered	No. of Days Out
1.	(179)	9-11	55
2.	(182)	10-10	24
3.	(176)	10-11	35
4.	(181)	10-10	21
5.	(174)	10-11	39
6.	(141)	9-10	37
7.	(185)	9-10	34
8.	(163A)	10-11	21
9.	(142)	9-11	58
10.	(135)	10-11	31
11.	(178)	11-11	12
12.	(160)	10-10	19
13.	(140)	10-11	31
14.	(162)	10-11	35

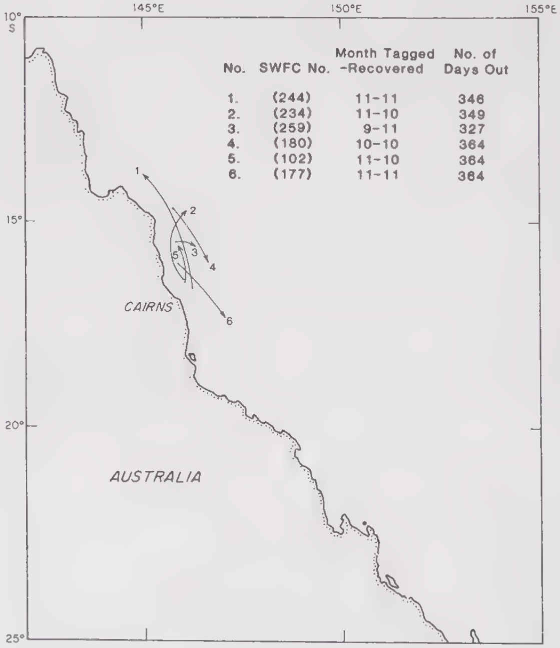
No.	SWFC No.	Month Tagged -Recovered	No. of Days Out
1.	(227)	10-11	41
2.	(219)	9-10	23
3.	(269)	9-10	19
4.	(245)	11-11	3
5.	(205)	9-10	29
6.	(228)	9-10	24
7.	(246)	9-11	56
8.	(231)	9-11	49

Figure 4.—Tag and recovery locations, 0-60 d time at large. Lines indicate point of tagging and recovery only.



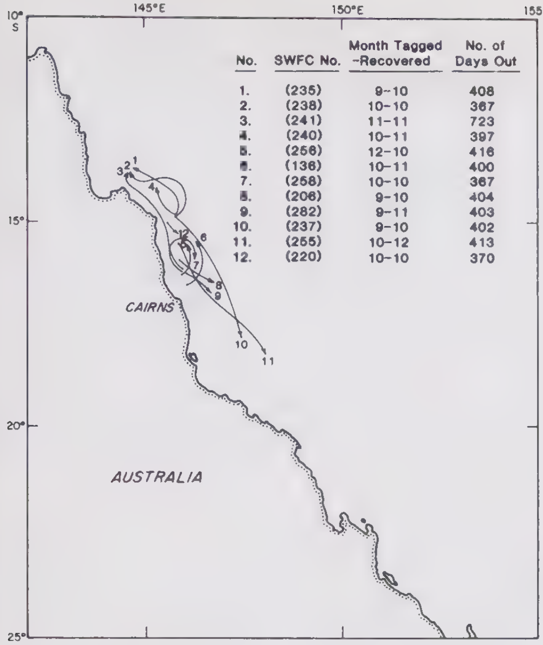
No.	SWFC No.	Month Tagged -Recovered	No. of Days Out
1.	(134)	8-10	61
2.	(243)	9-11	68
3.	(74)	10-1	95
4.	(184)	9-11	65

Figure 5.—Tag and recovery locations, 61-120 d time at large. Lines indicate point of tagging and recovery only.



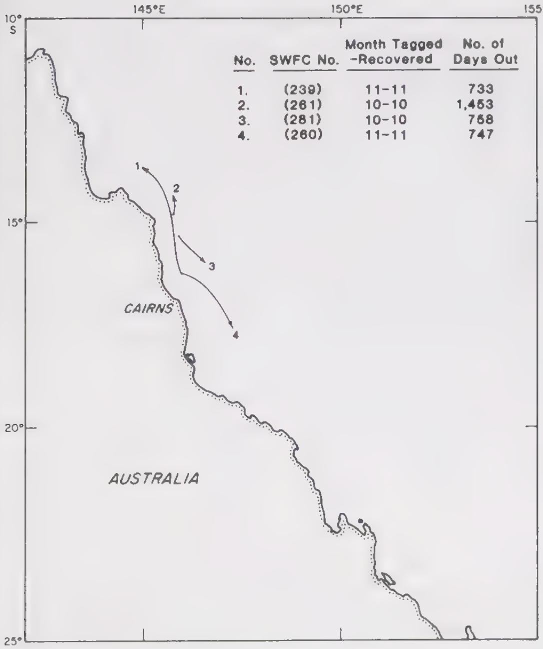
No.	SWFC No.	Month Tagged -Recovered	No. of Days Out
1.	(244)	11-11	346
2.	(234)	11-10	349
3.	(259)	9-11	327
4.	(180)	10-10	364
5.	(102)	11-10	364
6.	(177)	11-11	364

Figure 6.—Tag and recovery locations, 241-365 d time at large. Lines indicate point of tagging and recovery only.



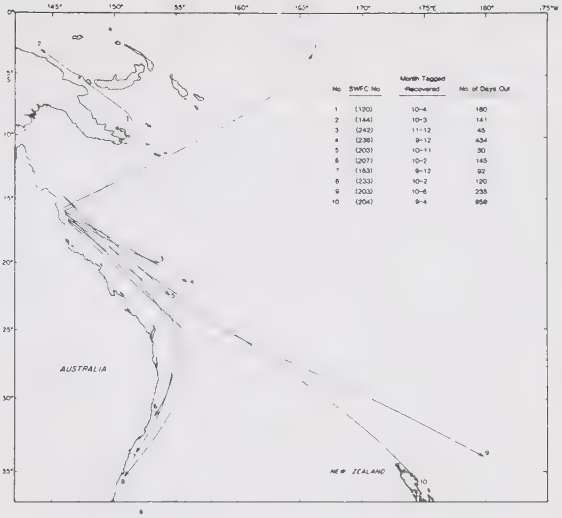
No.	SWFC No.	Month Tagged -Recovered	No. of Days Out
1.	(235)	9-10	408
2.	(238)	10-10	367
3.	(241)	11-11	723
4.	(240)	10-11	397
5.	(256)	12-10	416
6.	(136)	10-11	400
7.	(258)	10-10	367
8.	(206)	9-10	404
9.	(282)	9-11	403
10.	(237)	9-10	402
11.	(255)	10-12	413
12.	(220)	10-10	370

Figure 7.—Tag and recovery locations, 366d-2 yr time at large. Lines indicate point of tagging and recovery only.



No.	SWFC No.	Month Tagged -Recovered	No. of Days Out
1.	(239)	11-11	733
2.	(261)	10-10	1,453
3.	(281)	10-10	758
4.	(260)	11-11	747

Figure 8.—Tag and recovery locations, 2 to 3 yr and 3 to 4 yr time at large. Lines indicate point of tagging and recovery only.



No	SWFC No	Month Tagged -Recovered	No. of Days Out
1	(120)	10-4	180
2	(144)	10-3	141
3	(242)	11-12	45
4	(236)	9-12	434
5	(203)	10-11	30
6	(207)	10-2	145
7	(183)	9-12	92
8	(233)	10-2	120
9	(203)	10-6	235
10	(204)	9-4	959

Figure 9.—All recoveries 500 nmi or greater from location of tagging. Lines indicate point of tagging and recovery only.

average distances of tagging to recapture points increase from time of tagging for at least the first 180 d of time at large. A regression was calculated for recaptures made within the first 235 d from time of release. Recapture distances by number of days from release are given in Figure 10. The greatest recorded distance between tagging and recapture was 2,100 nmi, 235 d after release. Recaptures made near the tagging area (within 210 nmi) were common 1 and 2 yr after tagging (17 at 1 yr, 4 at 2 yr) and one recapture at nearly 4 yr after release (1,453 d or 3.98 yr).

The average migration rate in nautical miles per day (nmi/d) away from the location of tagging, for selected time periods subsequent to tagging, was calculated using two methods from data derived from time, straight line distance, and true bearing angle measurements from the tagging point to the recapture point. Of particular interest are the data obtained from recaptures within the first three time periods selected (0-60, 61-120, and 121-240 d) since these data may better define the average migration rate of black marlin away from a high population density (as reflected in CPUE) and reported spawning area. The greatest observed migration rate for any black marlin recaptured was 22.3 nmi/d, an average attained during a release time of 30 d. Average movement was calculated in nautical miles per day for the first three time periods, then multiplied by the average number of days within the period in relation to zero day, or start of the first time period, to obtain the approximate average distance of migration:

Days	*Midpoint in time*	*Avg. nmi/d*	*To period midpoint*
0-60	30	3.65	109.5 nmi
61-120	40	6.08	547.2 nmi
121-240	180	7.70	1,386.0 nmi

The percentage of recaptures by month of tagging was August 30%, September 30%, October 49%, November 17%, and December 2%. Recaptures made within the first period (0-60 d) were examined to determine the migration rate for black marlin tagged in September (9 fish recaptured), October (13 fish recaptured), and November (3 fish recaptured). No black marlin tagged in

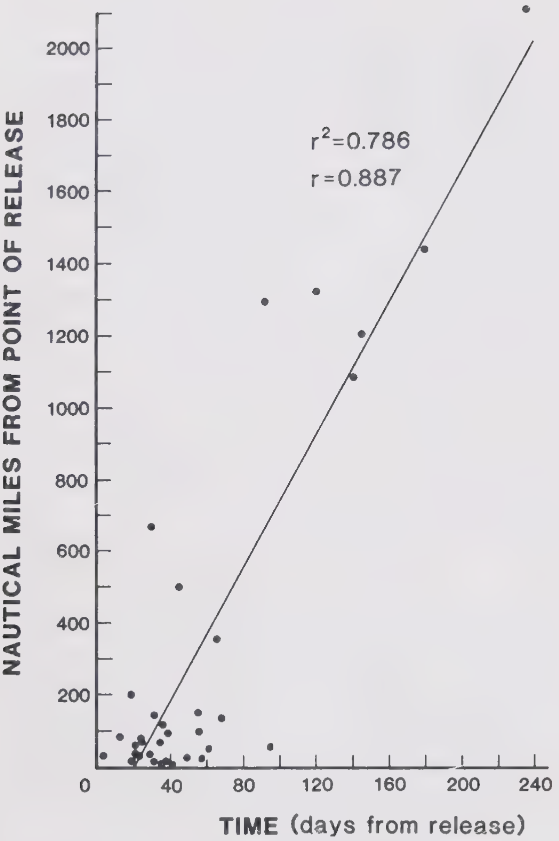


Figure 10.—Regression plot of black marlin recovery distances, by number of days at large.

August or December were recaptured within the first 60 d from release. The average rate of movement during the first 60 d from release for black marlin tagged in September was 1.46 nmi/d; October, 4.58 nmi/d; and November, 10.06 nmi/d. The average rate increased 3.1 times from September to October, and 2.2 times from October to November, with the November rate being 6.9 times that recorded for September. An increasing average rate of movement (nmi/d) was shown for black marlin tagged during the later part of the season. This may indicate that black marlin frequenting the general area of tagging early in the season may not migrate out of the area as rapidly as those black marlin tagged later in the season.

Vector analysis used distance and directional data determined by examination of tagging and recovery locations (straight-line distance), time of release (number of days), and direction (number of degrees, true bearing) from tagging point to recovery point. Vector mean bearings and distances were calculated 0-730 d in five time periods as shown in Figure 11. This analysis indicated a reduced rate of movement for the first time period after tagging (0-60 d) compared with the two following time periods (61-120 and 121-240 d). For the second period an acceleration of movement of 6.2 times the first period was noted. A reduced rate of movement of mean vector distance of 2.8 times the second period was observed for the third period (121-240 d).

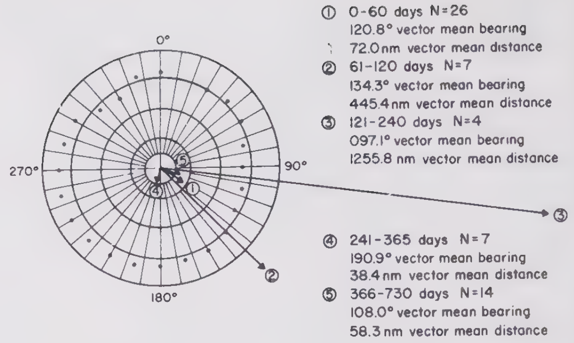

0°
90°
180°
270°
① 0-60 days N=26
120.8° vector mean bearing
72.0 nm vector mean distance
② 61-120 days N=7
134.3° vector mean bearing
445.4 nm vector mean distance
③ 121-240 days N=4
097.1° vector mean bearing
1255.8 nm vector mean distance
④ 241-365 days N=7
190.9° vector mean bearing
38.4 nm vector mean distance
⑤ 366-730 days N=14
108.0° vector mean bearing
58.3 nm vector mean distance

Figure 11.—Vector mean bearings and distances for five recovery periods: 0-60 d, 61-120 d, 121-240 d, 241-365 d, and 366-730 d.

Arcs showing mileage limits were plotted, using both the average distance traveled from tagging to recovery per day by period, times the midpoint for each time period; the vector mean distance for each period is given in Figure 12. The differences between the plots of average nautical miles per day and the vector mean distance are relatively small. Vector mileage arcs are smaller due to the method of calculation. The black marlin covering the most distance from the point of tagging (2,100 nmi in 235 d) to the recapture site northeast of New Zealand (see Fig. 12) had an average daily rate of travel of 8.94 nmi.

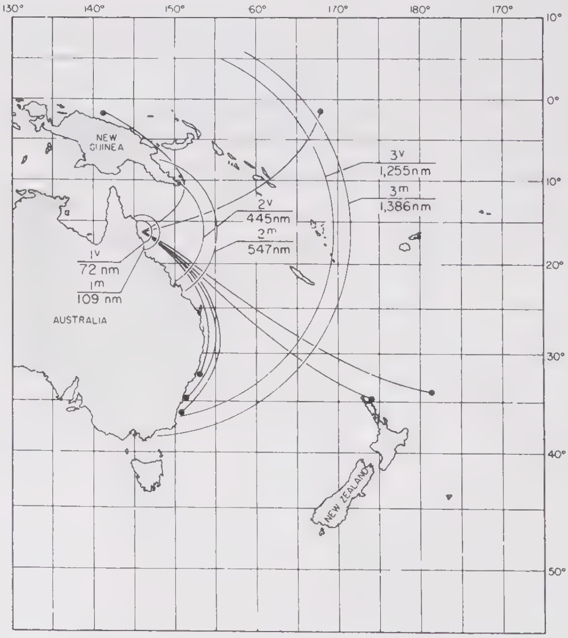


Figure 12.—Nautical mile arcs for average distance traveled from tagging to recovery by time periods, (1 = 0-60 d, avg. 30 d; 2 = 61-120 d, avg. 90 d; 3 = 121-240 d, avg. 180 d). V is the vector mean distance for each period, m is the measured distance. Only long distance recoveries (< 500 nmi) are also shown.

Studies by Ueyanagi (1960) indicate that a black marlin may spawn in the northwestern Coral Sea in early summer (November). Recaptures are reported in the spring and early summer near the point of tagging about 1, 2, 3, and 4 yr after tagging. This would indicate that at least some of these black marlin tagged show a returning migration trend toward a suspected spawning area.

Geographical areas fished by commercial longline gear vary in amount of fishing effort expended and changes in longline effort may affect the number of recoveries and recovery location. From 1965 to 1975, black marlin catch rates from the Japanese longline fishery in many areas of the southwest Pacific averaged 2.1-5.1 + and >5.1 fish/1,000 hooks effective hooking effort (Suzuki and Honma 1977); peak hooking rates were recorded near the tagging area off north Queensland from October through December. The distribution of longline effort and CPUE should be reflected in the distribution of recovery locations for black marlin tagged in the western Coral Sea. The effective effort for black marlin fished in the Coral Sea is high. The effectiveness index (*E*) of the effort on black marlin (effective hook/nominal hooks) exceeds 1.0 in 19 of 24 yr (1952-75) as reported by Suzuki and Honma (1977).

Figure 13 outlines the 10-yr average level of Japanese longline fishing effort by 5° longitude and 5° latitude for the Coral Sea and adjacent areas from 1968 to 1977 (Anonymous 1970-79). Extensive longline fishing effort is evident north of the Solomon Islands, east of Queensland, and off the southeast coast of Victoria, Australia, and off the eastern coast of New Zealand. A substantial amount of longline effort was expended off the Great Barrier Reef area (north Queensland) from lat. 20°S northward. No longline effort is reported in the eastern Arafura Sea and Torres Strait between Cape York and Papua. Fishing effort isolines also indicate an area of reduced effort extending from near New Caledonia eastward, centering on about lat. 20°S. The effort levels for the 5° areas given in Figure 13 for the period 1968-77 are indicated by numbers of hooks fished × 10⁴. The strata of hook effort, levels 1-3, representing 9-99, 100-199, and 200 or greater × 10⁴, respectively, were averaged for the 1968-77 period.

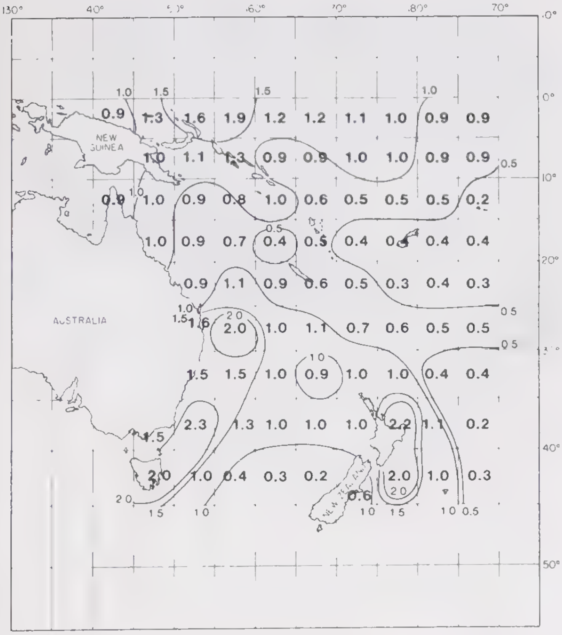


Figure 13.—Average distribution of Japanese longline fishing effort for 1968-77 by 5° longitude × latitude areas from Japanese Fishery Agency data. Effort levels for the 10-yr period were determined by averaging effort level 0-99, 100-199, 200 or greater × 10⁴ hooks in terms of 1 = 0-99, 2 = 100-199, and 3 = 200 or greater × 10⁴ hooks.

The distributions of longline fishing CPUE for black marlin as a measure of apparent abundance in the area from near northern New Zealand, and near the New Guinea-Solomon Islands are shown in Figure 14a, b, c (from Suzuki and Honma 1977).

A review of CPUE for June-August (Fig. 14a) shows CPUE levels of 0.6-2.0 black marlin/1,000 hooks are common in the New Guinea-Bismark Archipelago-Solomon Islands area throughout the winter months. Average effort levels are high in this area, 100-199 hooks × 10⁴ per 5° longitude × 5° latitude area. In September-November (Fig. 14a, b) the tagging area has a high CPUE. The first indications of a poleward shift of high CPUE areas for black marlin, in the range of 0.6-2.0 fish/1,000 hooks along the western coast of the Coral Sea, occurs during September. By examining the changes in CPUE for the area off north Queensland during and after the months of September, October, and November, some insight into the shift of high black marlin CPUE away from the tagging areas can be observed. High catch rates (≥5.1 black marlin/1,000 hooks) are common in the western Coral Sea from lat. 10° to 20°S in October and November. The high CPUE areas for September-November are near long. 150°E × lat. 15°S and have a hook effort of <99 hooks × 10⁴ per 5° longitude × 5° latitude area. In December (Fig. 14b), increasing catch rates are observed south to about lat. 25°S. These higher catch rates are observed to the west within a latitudinal band of lat. 15° to 20°S. Longline hook effort level is <99 hooks × 10⁴ per 5° longitude × 5° latitude area. In January (Fig. 14b), catch rates increase along the Australian coast to about lat. 35°S. Catch rates per 5° square are lower than those observed previously off the north Queensland area (lat. 10° to 20°S), but remain in the range of 2.1-5.0 black marlin/1,000 hooks. The center of high black marlin CPUE is in an area having an effort level of <99 hooks × 10⁴ per 5° longitude × 5° latitude. By February (Fig. 14c), black marlin CPUE in the lat. 15° to 20°S area has decreased to 0.5 black marlin/1,000 hooks. The high CPUE areas continue to be off the Queensland and New South Wales coast, from lat. 20° to 35°S. Average effort levels in the high CPUE areas for February are at a higher level than during the previous months, ≥100 hooks per 5° longitude × 5° latitude area but <199 hooks × 10⁴ per 5° area. CPUE patterns for March (Fig. 14c) change considerably, with higher CPUE areas noted north of lat. 15°S, and reduction in high CPUE areas to the south. Catch rates averaged 0.6-2.0 black marlin/1,000 hooks per 5° longitude × 5° latitude area. Effort levels in the higher CPUE areas are less than averages observed for high CPUE areas in February, and average ≤99 hooks × 10⁴ per 5° longitude × 5° latitude area. Most catches in April (Fig. 14c) are being made north of lat. 20°S. Catches average 0.6-2.0 fish/hooks per 5° longitude × 5° latitude area. A further retraction of high CPUE areas from latitudes south of 15°S is evident in May (Fig. 14c). Some catches at levels of 0.6-2.0 black marlin/1,000 hooks are observed for areas east of the Queensland coast, but the center area of high CPUE is in the New Guinea-Bismark Archipelago-Solomon Islands area. Average effort levels are higher in this area and are between 100 and 199 hooks × 10⁴ per 5° longitude × 5° latitude square.

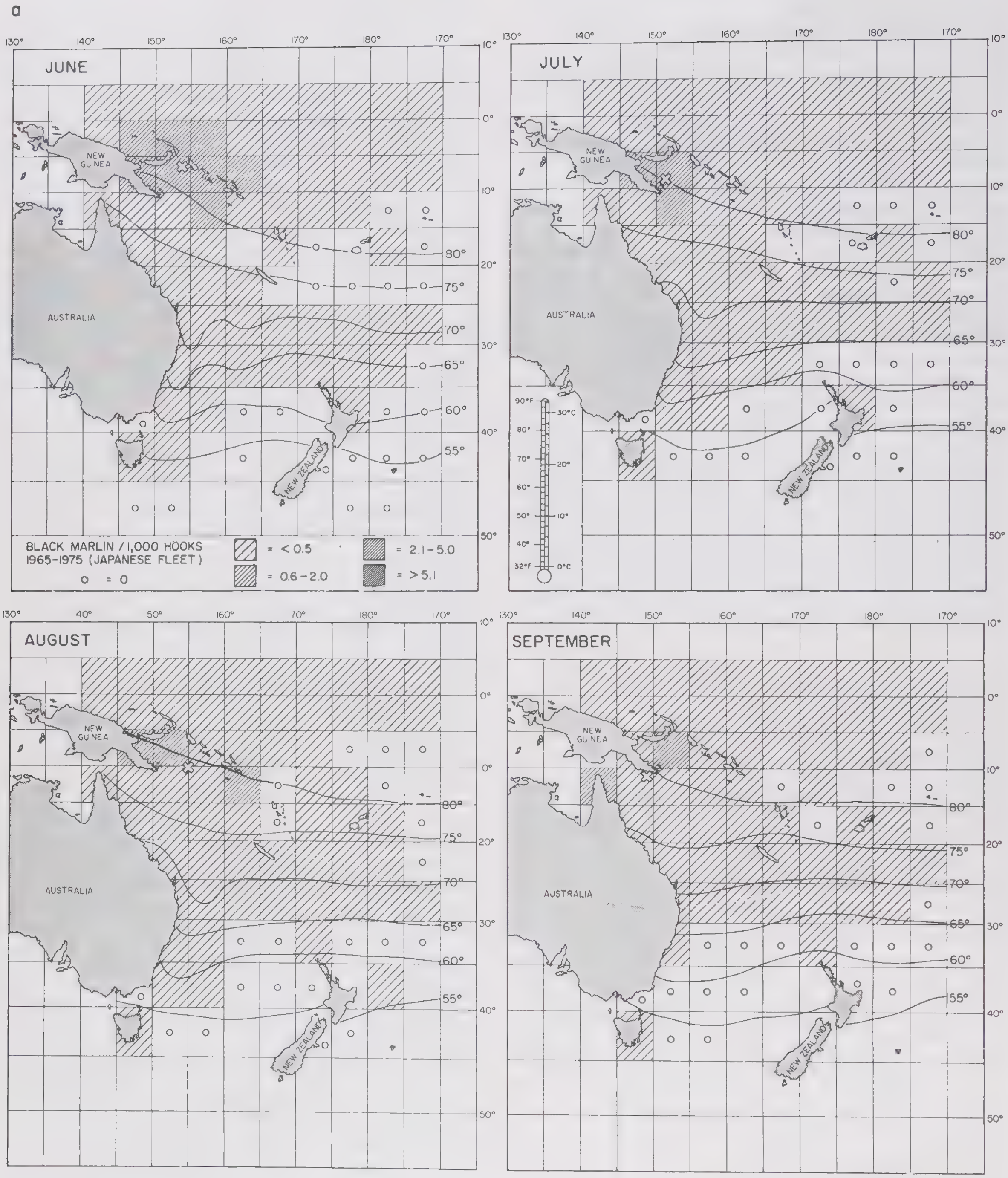


Figure 14.—Distribution of average hook rates for black marlin per 1,000 hooks effective effort (from Suzuki and Honma 1977): a. June-September. b. October-January. c. February-May.

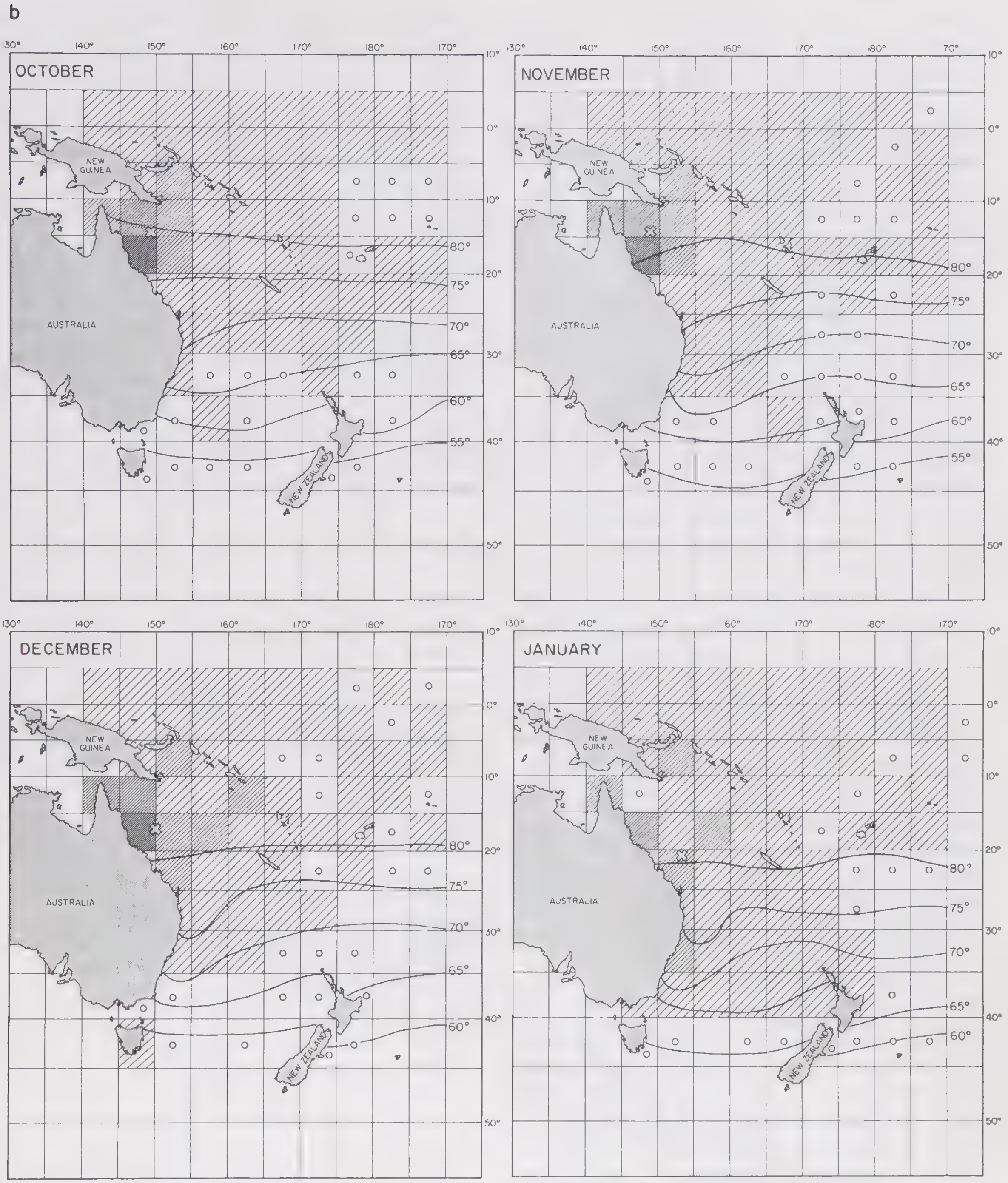


Figure 14.—*Continued.*

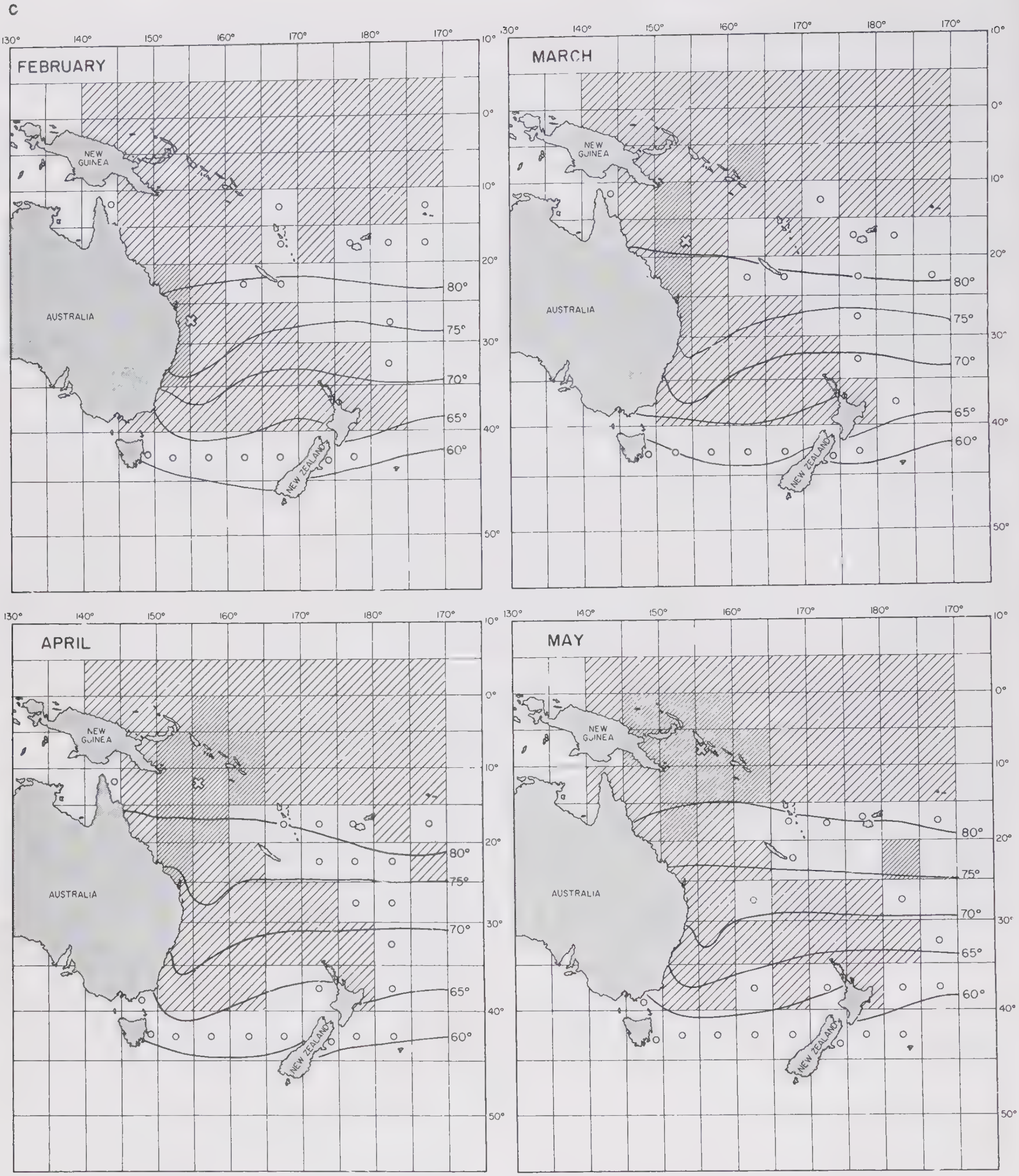


Figure 14.—*Continued.*

Low CPUE levels of black marlin, < 0.5 marlin/1,000 hooks, are common throughout most of the southwest Pacific from lat. 30°S northward during every month of the year. The southerly limit in the summer through fall (January-May) is about lat. 40°S. The only area commonly showing a low CPUE level throughout the year is the area from New Caledonia east, in a latitudinal band of lat. 10° to 20°S. A retraction of the low CPUE levels to the northwest from the New Zealand area is observed in October through December. CPUE data indicate that minor catches of black marlin could be expected in many areas of the southwest Pacific in most months.

To better define the changes in areas of high CPUE, the approximate center of high CPUE was estimated and its geographical position by month is given in Figure 15. A progressive southward movement of high CPUE areas from the tagging area is observed for December and January, reaching its southern-most limit by February. A substantial geographical shift in high CPUE center from about lat. 28° to 18°S has occured. In April, the shift is northeastward to the Solomon Islands area (lat. 10°S). CPUE center moves northwestward to about lat. 5°S in May and June. The southward movement is again evident in July-September, shifting the high CPUE center from lat. 5°S to about lat. 10° to 11°S between New Guinea and the Solomon Islands.

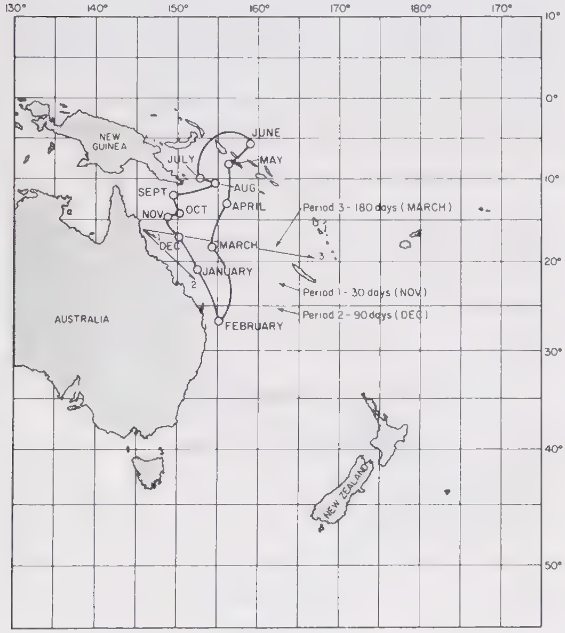


Figure 15.—Monthly movements of the approximate center (as determined by eye-fit) of high longline CPUE for black marlin as observed in Figure 14a, b, c.

DISCUSSION AND SUMMARY

The north Queensland, Australia, area is one of the most productive locations in the Pacific for anglers using rod-and-reel to catch black marlin. The excellent fishing attracts anglers from about the world, as indicated by the several countries represented in the tag recovery summary (see Table 2). An important factor was that many of the anglers and charterboat operators in this area were willing to tag and release black marlin. The number of black marlin tagged off north Queensland (2,576) is the sum of tag report forms returned by cooperating anglers. This represents a minimum number of fish tagged, since some report forms are not returned to the tagging agency (Squire 1974). The extent of nonreporting of releases is assumed to be minimal in this area because of the excellent management of the tagging effort by the Cairns Game Fishing Club which distributed the tagging equipment and maintained accurate records.

Of the black marlin reported tagged during 1968-78, 60 tags were returned for an overall return rate of 2.3%. The maximum return rate was observed in 1974, 5.1% for 335 marlin tagged with H-type tags. This is a greater return rate than the 0.9% rate experienced for striped marlin tagged by anglers in the northeastern Pacific (Squire 1974). For recapture data having information on sex, 89% were reported to be males.

The average weight of black marlin, as estimated at the time of tagging, was approximately 175 kg (385 lb) each. Table 5 indicates that substantial overestimates of black marlin weight at tagging were recorded. The ability of an angler to estimate accurately the weight of a large fish such as a black marlin actively swimming in the water is subject to considerable error. The data presented indicate that a reasonable level of accuracy (one that might produce growth rate data or allow estimates of annual average size) is not possible without the application of correction values. Estimated weight data, given by average weight per year (Fig. 3), indicate that estimated weights peaked in 1974 at 201 kg (445 lb)/fish. Average shoreside landing weights, as recorded by the Cairns Game Fishing Club, are about twice the estimated average weight of tagged fish (Table 4). This would indicate that the fish being landed for weighing are the large ones, and are not representative of the average weight of all marlin caught. Landing larger marlin, rather than tagging and releasing them, would tend to bias the average estimated tagging weight lower. Figure 3 also shows an increase in tagging effort northward along the Great Barrier Reef to latitudes < 15°30′S from the area immediate to Cairns, Australia (lat. 17°S). This increase in tagging is evident in the latitudinal band 15°30′ to 14°30′S, beginning in 1972.

The fish recaptured at 1, 2, and 3 yr after tagging, were recaptured relatively close to the point of tagging. Fish released about 1 yr earlier were recovered a mean distance of 38.4 nmi, and 2 yr earlier, at 58.3 nmi, from the point of tagging. The recovery of tagged fish at annual increments near the tagging location indicates that there is a tendency for at least some tagged black marlin to return to the northwestern Coral Sea.

To better define seasonal migratory patterns, tagging effort should be distributed throughout the species range. In most cases where tagging of oceanic species is conducted, the ideal distribution is not achieved. The tagging effort reported on in this paper is from one portion of the black marlin distributional range in the western Pacific and the associated Indo-Pacific area (Fig. 1). Black marlin are presumed to spawn in the Coral Sea between October and December (Ueyanagi 1960), and tagging takes place at this time at or near the spawning area. Black marlin are usually caught by anglers in proximity to the outer edge of the Great Barrier Reef, and most tagging takes place in this area. The commercial longline fishing operations take place offshore from the tagging area. The tagging area is within the high black marlin CPUE area for commercial longline gear during the September-December period (see Fig. 14a, b, c) and is also within an area of moderately high longline effort (see Fig. 13). Because of the commercial longline effort in this area, a number of short-term (0-60 d) recoveries were obtained. Of importance in evaluating the tag return data for migratory patterns is the relationship between a shift of the high CPUE areas and the frequency of recoveries in these areas. Recoveries about 6 mo, and 1 or more years after tagging, are most important, if one is to assume a seasonal migratory pattern exists.

Most of the tag and recovery geographical plots given in Figures 5 to 10 tend to give the impression that all migration is radiating outward from a geographically localized point of tagging, and that the tagging location is the "center" of distribution; this is not the case. Black marlin are tagged in an area as they migrate through it at varying rates and directions.

Emigration from the area of tagging during the first few months appears, for most recoveries, to be toward the south-southeast. An overall mid-point average for the first 0-60 d of release ($\bar{x}$ = 30 d) was 109 nmi; for period 2, 61-120 d ($\bar{x}$ = 90 d), 547 nmi; and for period 3, 121-240 d ($\bar{x}$ = 180 d), 1,386 nmi. Arc distances given in Figure 12 show that, based on average distance/time (180 d and 1,386 nmi), the average distance of migration would be from about southern New South Wales, just east of the New Hebrides, northeast to midway between Solomon Island and the Gilbert Islands to the Equator. The longest distance recorded was to the southeast of the tagging area, east of New Zealand (2,100 nmi, or 8.9 nmi/d). For black marlin recovered 121-240 d after tagging, the average rate was 7.7 nmi/d and in the time period of 180 d the average distance traveled at that rate would be 1,386 nmi. However, this sample, having a release time of 0-240 d, represents only 13.5% of the total recoveries. Based on average migration rate data, black marlin tagged early in the season (September) tended to migrate away from the point of tagging at a lower average rate for the first time period (0-60 d) than black marlin tagged in October, November, or later in the fishing season. This may be because the tagging areas are in or near the spawning area, and the behavior of black marlin in this area earlier in the spawning season may be different from those entering later in the season.

Data obtained from this study indicate that black marlin tagged in the western Coral Sea do not undergo short-term trans-Pacific migrations, although some interchange over time with the eastern Pacific is possible. The degree of interchange with the Indo-Pacific is unclear. Emigration from the tagging area to north of New Guinea was recorded; however, no recoveries were recorded to the east in the Arafura, Banda, or Timor Seas or the eastern Indian Ocean.

Some tentative estimate of the central tendency of migration direction and rate can be made using the vector analysis (Fig. 11), the graphic plots of tag and recovery points (Figs. 4 to 9), and movements of high CPUE areas over time (Fig. 14a, b, c), in relation to the geographical distribution of longline effort levels in the southwest Pacific (Fig. 13). Figure 15 gives the approximate geographical centers of high longline CPUE by month as observed in data presented in Figure 14a, b, c. Inspection of the longline CPUE rates for the 5° areas and plots of geographical location indicate south or southeast movement from the tagging area in the summer and then a northward movement of high CPUE areas to the New Guinea-Bismark Archipelago-Solomon Islands area in the winter. Vector mean bearing and distance data from tag results were plotted in Figure 11 and indicate direction and distance of migration away from the tagging area for 30, 90, and 180 d from October, the month having the most tagging activity (49%).

Monthly average sea surface temperature isotherms are shown in Figure 14a, b, c. High longline CPUE areas for black marlin are located in close relation to the 26.7°C (80°F) average isotherm during most months of the year. High CPUE areas are related to lower temperatures and are found between the 23.9°C (75°F) and 26.7°C (80°F) isotherms only in February off the Queensland and New South Wales coasts. Latitudinal warming and cooling as reflected in sea surface temperature may be a measure of other physical or biological environmental parameters that may be important to black marlin distribution.

From the results of tagging (emigration rates and directions), inspection of average longline effort, and CPUE, a diagramatic description of black marlin migration in the southwestern Pacific can be hypothesized (Fig. 16). The tagging results indicate that the migratory rates and patterns of black marlin are highly variable. There is, however, a central tendency of movement of tagged fish not unlike that expected from observations of the movements of CPUE trends. Black marlin were observed to move southward from the tagging area toward southeastern Australia and New Zealand in late summer, then northeast toward the Gilbert Islands, and to northeast of New Guinea in the winter, returning to the western Coral Sea in the spring and early summer. The interchange rate of the population found in the Coral Sea, with the population of the Indo-Pacific area, is unclear. The relationship of the Coral Sea population to that in the central Pacific and other areas in the western Pacific is also not defined. Though no recoveries have been made in these areas, some population interchange could be expected.

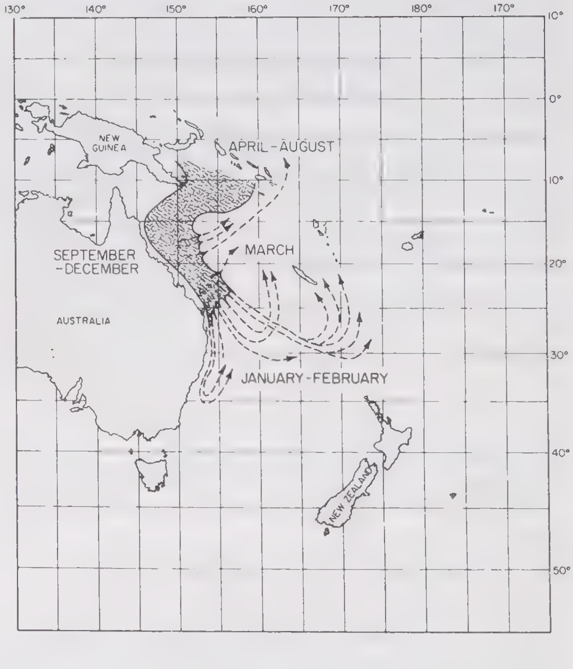


Figure 16.—A hypothetical description of black marlin migration in the southwest Pacific Ocean.

ACKNOWLEDGMENTS

The cooperation of the marine anglers who caught, tagged, and released black marlin made this study possible. We wish to convey our appreciation to the marine anglers, and to the Japanese and Korean commercial longline fleet captains and crews who recaptured tagged marlin and returned the tags.

Many of the recoveries were returned through either the Far Seas Fisheries Research Laboratory, Shimizu, Japan, or the Kanagawa Prefectural Fisheries Experimental Station, Joga Shima, Kanagawa Prefecture, Japan. We are grateful to scientists Eiji Hanamoto of the Kanagawa Fisheries Experimental Station, and Shoji Ueyanagi, Susumu Kume, and Shoji Kikawa of the Far Seas Fisheries Research Laboratory for their assistance in return of marlin tags and information used in the analysis. The interest of the charterboat captain in learning more about the resource on which he fishes often results in the marlin being tagged, although the anglers are credited for tagging and releasing the marlin. To the charterboat fleet off Cairns and nearby areas, our sincerest appreciation.

The Cairns Game Fishing Club provided excellent control of tagging equipment and maintained complete and accurate records of tagged fish throughout the years, thereby making the tagging analysis more accurate. Their precision handling of the program is appreciated.

To Julian Pepperell of New South Wales State Fisheries, who furnished a portion of the data used in this analysis, our sincere appreciation. The efforts of Norman Bartoo and Richard Evans (SWFC) in statistical analysis of the data are acknowledged. To others such as the International Game Fish Association and marine game fish anglers throughout the world who gave their support, we thank you.

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CALIBRATION OF NORTHERN ANCHOVY SPAWNING BIOMASS ESTIMATES DERIVED BY EGG PRODUCTION AND LARVAL CENSUS METHODS

GARY D. STAUFFER[1]
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038

ABSTRACT

A mathematical procedure is developed for converting estimates of northern anchovy spawning biomass derived by egg production methods to values equivalent to those derived by larval census methods. This calibration is based on the results of concurrent spawning biomass surveys conducted for both methods in 1980 and 1981. Two egg production surveys were made in 1981. The coefficient of proportionality for the two biomass estimators is not a simple constant but a function of egg survival, daily population fecundity, and larval mortality rate—all of which may vary from year to year. The common link between these two biomass estimators is the daily production of larvae at the time of hatching. The coefficient of proportionality between the hatching rates derived from the two estimators is relatively constant for the three test cases. The proposed equation for converting egg production estimates of spawning biomass to equivalent larval census estimates may result in a bias of 3.1% in the equivalent larval census estimate.

RESUMEN

Se desarrolla un procedimiento matemático para convertir estimaciones de la biomasa de la puesta de *Engraulis mordax* (anchoa), derivado de los métodos equivalentes para la producción de huevos y del censo larval. Esta calibración está basada en los resultados obtenidos sobre la biomasa de la puesta utilizando ambos métodos, durante exploraciones en 1980 y 1981. En 1981 se efectuaron dos exploraciones para determinar la producción de huevos. El coeficiente de proporcionalidad para los dos valores en la estimación de la biomasa, no es una constante simple, sino una función de la supervivencia de huevos, fecundidad diaria de la población y valor de la mortalidad larval, factores que varían de un año para otro. El eslabón común entre estas dos estimaciones de la biomasa es la eclosión diaria de larvas. El coeficiente de proporcionalidad entre los valores de eclosión derivados de los dos valores estimados resultó relativamente constante para las tres pruebas efectuadas. La ecuación que se propone para convertir la estimación de la producción de huevos en la estimación de la biomasa de la puesta y la estimación equivalente del censo de larvas, puede resultar con una desviación del 3.1% en la estimación equivalente del censo de larvas.

INTRODUCTION

The Fishery Management Plan (FMP) for northern anchovy specifies the seasonal catch quota for the U.S. fishery off California based on an annual estimate of anchovy spawning biomass. The quota formula options presented in the original FMP were evaluated using an anchovy population model developed from the 1951-75 time series of larval census estimates (Smith 1972; Huppert et al. 1980). The La Jolla laboratory of the Southwest Fisheries Center (SWFC), National Marine Fisheries Service, is responsible for making these annual estimates. Parker (1980) described and demonstrated the feasibility of a new method of estimating anchovy spawning biomass referred to as the egg production method. In 1980 the SWFC conducted concurrent surveys to estimate spawning biomass by both methods (Stauffer and Picquelle 1981; and MS[2]). The results indicated that the value of the egg production estimate may be 50% to 60% of the corresponding larval census estimate. Because of the advantages of the egg production method[2]—particularly fewer vessel days at sea—the SWFC decided to convert the annual surveys to the egg production method by 1982 and to conduct concurrent surveys by the two methods in 1981.

The Pacific Council instructed the anchovy plan development team to modify the FMP and to fit the anchovy population model to a time series of spawning biomass estimates equivalent to the egg production method. The council also requested that the SWFC convert the egg production estimates to equivalent larval census estimates in the intervening years until the new plan is implemented. The purpose of this report is to document the procedure for converting egg production estimates to equivalent larval census estimates beginning in 1982, based on the concurrent surveys of 1980 and 1981.

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[1] Present address: Northwest and Alaska Fisheries Center, 2725 Montlake Boulevard East, Seattle Washington 98112

[Manuscript received February 14, 1983.]

[2] Stauffer, G. D., and S. J. Picquelle. MS. Egg production estimates of spawning biomass of the northern anchovy, *Engraulis mordax*, for 1980 and 1981. Southwest Fisheries Center, La Jolla California.

DERIVATION OF CALIBRATION

Simple Case of Proportionality

The basis for the calibration between the two spawning biomass estimators is that the larval census estimate, B_1, is proportional to the egg production estimate, B_e, for any year in which concurrent surveys have been conducted. This can be described by

$$B_1 = c\,B_e, \tag{1}$$

where c is a coefficient of proportionality. If c is constant from year to year then the larval census estimate in year j can be derived from an egg production estimate from equation (1) where c is estimated for the calibration years. This conversion equation becomes more complex if c is quite variable from year to year, violating the assumption of constant proportionality.

Complex Case of Variable Proportionality

The calibration in the case when c is not equal from year to year can be derived from the relationship of the larval census estimate, B_1, to the daily production of newly hatched larvae, L_h, and from the relationship of the egg production estimate, B_e, to daily rate of hatching eggs, P_h. A common link between these two biomass estimators is the daily production of larvae at the time of hatching. The production of larvae estimated from the plankton data collected on the larval census survey should be proportional to the daily rate of hatching eggs estimated from the plankton data collected on the egg production survey. This says that

$$L_h = b\,P_h, \tag{2}$$

where b is a constant of proportionality. The value of b would be 1.0 if the two survey methods give equivalent estimates of L_h and P_h. The conversion from one biomass estimator to the other can be specified by expressing L_h and P_h as functions of B_1 and B_e, respectively.

Daily production of larvae. Lo[3] has found that the survival of anchovy larvae increases with age such that the instantaneous rate of mortality is not constant, as previously considered (Hewitt 1982). She modeled the decay in a daily cohort of larvae, $L'(a)$ as:

$$\frac{dL'(a)}{da} = -\frac{\beta}{a} L'(a) \tag{3}$$

where a is age of larvae with time zero at fertilization, and β is the mortality coefficient. The number of larvae within a cohort at age a is the intregral of (3)

$$L'(a) = L'_h \left(\frac{a}{a_h}\right)^{-\beta} \tag{4}$$

where L'_h is the number of larvae hatched, and a_h is their age at hatching.

For the larval census estimate of spawning biomass, Smith (1972) derived B_1 proportional to the census of larvae, L, for the year, that is,

$$B_1 = 8.9 \times 10^{-8} L, \tag{5}$$

where B_1 is in units of metric tons. The computation of the larval census, L, can be modeled as the quarterly sum of the integral of the larval mortality function (5), that is,

$$L = \sum_{i=1}^{4} L_i = \sum_{i=1}^{4} \int_{a_h}^{A} L_{hi}(t) \left(\frac{a}{a_h}\right)^{-\beta_i(t)} da$$

where $L_{hi}(t)$ is the daily production of newly hatched larvae on day t, quarter i, $\beta_i(t)$ is the mortality coefficient on day t, quarter i, and A is the maximum age larvae are effectively sampled by plankton net (505-micrometer-mesh bongo).

Solving this integral, the quarterly larval census, L_i, is equivalent to

$$L_i = \frac{L_{hi}\,a_h}{\beta_i - 1}\left(1 - \left(\frac{a_h}{A}\right)^{\beta_i - 1}\right),$$

assuming $L_{hi}(t)$ and $\beta_i(t)$ are constant for quarter i. Since the sum of the larval census for the summer and fall quarters is about 6% of the sum for the winter and spring quarters (Stauffer and Parker 1980), the annual larval census can be approximated by a function of winter-spring average production of larvae, L_h, and larval mortality rate, β, that is,

$$L = 2.12\,\frac{L_h a_h}{\beta - 1}\left(1 - \left(\frac{a_h}{A}\right)^{\beta - 1}\right).$$

Substituting for L into (5) and solving for L_h gives

$$L_h = \frac{B_1}{18.9 \times 10^{-8}} \left(\frac{\beta - 1}{a_h}\right)\left(1 - \left(\frac{a_h}{A}\right)^{\beta - 1}\right)^{-1} \tag{6}$$

Daily rate of hatching eggs. The egg production estimator, B_e, from Parker (1980) and Stauffer and Picquelle[4] is

$$B_e = \frac{k_1 k_2\ PW}{R\,F\,S}, \tag{7}$$

where k_1 is the geographic area for the stock, k_2 is conversion from grams to metric tons, P is daily rate of egg production in the sea per 0.05 m^2 surface area, W is average weight of female anchovies, R is fraction of females in the stock, F is batch fecundity per fish, and S is fraction of female fish spawning per day.

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[3] Lo, N C H MS Egg production of the central stock of northern anchovy, 1951-1982 NMFS, Southwest Fisheries Center, La Jolla, California

[4] See footnote 2.

By combining parameters so that the daily egg production in the sea for the anchovy stock is

$$P' = k_1 P$$

and the daily production of eggs per ton of adult fish or daily population fecundity is

$$p = RFS/WK_2,$$

equation (7) simplifies to

$$B_e = P'/p. \tag{8}$$

The daily rate of hatching eggs, P_h, can be estimated from the exponential egg mortality model,

$$P_h = P'e^{-Za_h} = P's$$

where Z is egg mortality rate, and s is total egg survival over the incubation period.

Substituting into (8) and solving for P_h gives

$$P_h = B_e\, p\, s. \tag{9}$$

Calibration equation. The equation for converting from the egg production biomass estimate to the larval census estimate is obtained by substituting L_h from (6) and P_h from (9) into (2) and solving for B_1. This gives

$$B_1 = b(18.9 \times 10^{-8}) \\ B_e \left(\frac{a_h}{\beta - 1}\right)\left(-1\left(\frac{a_h}{A}\right)^{\beta - 1}\right) ps \;. \tag{10}$$

The coefficient of proportionality, c, from equation (1) is now

$$c = b(18.9 \times 10^{-8}) \\ \left(\frac{a_h}{\beta - 1}\right)\left(-1\left(\frac{a_h}{A}\right)^{\beta - 1}\right) ps \;. \tag{11}$$

The source of any variability in the coefficient c from year to year, other than sampling error, should be due to changes in larval mortality rate, egg survival rate, the production of eggs per unit weight of adult fish, or departures from the assumed egg and larval mortality functions.

In any year with an egg production survey, an equivalent larval census estimate of spawning biomass can be derived from equation (10) using a value of b estimated from the calibration years 1980 and 1981. If an estimate of larval mortality rate, β, equivalent to estimates derived from the analysis of larval data is not available, then a value of β must be assumed. In addition, simplification of equation (10) is possible by substituting P' for pB_e from equation (8), giving

$$B_1 = b(18.9 \times 10^{-8}) \\ P's \left(\frac{a_h}{\beta - 1}\right)\left(-1\left(\frac{a_h}{A}\right)^{\beta - 1}\right) \;. \tag{12}$$

This says that the larval census estimate can be estimated from just an ichthyoplankton survey of anchovy eggs and an assumption of larval mortality. A survey of adult fish, then, is only necessary if an egg production estimate of biomass is also desired.

ESTIMATION OF CALIBRATION COEFFICIENTS

The calibration between the two anchovy biomass estimation methods can be evaluated from the paired surveys of 1980 and 1981. The estimates of the biomass and related parameters for the larval census and egg production methods are reported by Stauffer and Picquelle (1981; also footnote 2), Stauffer and Charter (1982), and Picquelle and Hewitt (1983). These estimates are summarized in Table 1. The larval census estimates of biomass are 1,611,000 metric tons (MT) and 2,544,000 MT for 1980 and 1981, respectively. The egg production estimates of biomass are 782,000 MT in 1980, 585,000 MT for the February 1981 survey, and 343,000 MT for the second 1981 survey (April). The coefficient of proportionality, c, from equation (1) is 2.06, 4.35, and 7.42 for the three surveys, respectively. The changes in c for the two

TABLE 1

Estimates of Parameters, Spawning Biomass, and Coefficients of Proportionality for Three Calibration Surveys

Parameter estimates	Units	March 1980	February 1981	April 1981
P	$\frac{\text{egg}}{\text{tow day}}$	10.09	7.961	4.936
P'	$\frac{10^{12}\text{ eggs}}{\text{day}}$	23.97	19.01	11.46
p	$\frac{10^{6}\text{ eggs}}{\text{ton day}}$	30.65	32.60	33.46
Z		0.453	0.138	0
a_h	Days	2.71	2.75	2.75
s		0.293	0.684	1.000
β[1]		1.7999	1.7056	1.7085
B_e	Metric tons	782,000	585,000	343,000
B	Metric tons	1,611,000	2,544,000	2,544,000
c		2.06	4.35	7.42
b		0.4195	0.3249	0.3699

$\bar{b} = 0.3835$

[1] Parameter values for β are taken from Picquelle and Hewitt (1983)

1981 surveys with respect to the 1980 calibration amount to a 111% and a 260% increase. This variation in c is primarily due to the large differences in egg survival, since the other parameters in (11) are relatively constant (Table 1). These large differences in c suggest that the calibration between the two biomass methods using equation (1), which assumes c is constant year to year, is rather poor.

Analysis of the calibration based on equation (10) provides relatively consistent values of the constant of proportionality, b. The values of b for the three comparisons are 0.4195 for 1980, 0.3249 for February 1981, and 0.3699 for April 1981—a maximum decrease of 23% relative to the 1980 value. These values of b are much lower than 1.0. Based on equation (2) this implies that larval production estimated from the larval data is about 38% of the value derived from the egg data. The differences between L_h (production of larvae) and P_h (rate of hatching eggs) for 1980 surveys are illustrated in Figure 1. The daily rate of hatching eggs was approximately 3.7 eggs/tow (0.05 m^2 of sea-surface area). The daily production of larvae is about 42% of the value P_h. Possible explanations for this consistent empirical value of b less than 1.0 are that the estimate of L_h is averaged over winter and spring months, whereas P_h is the average of one month during the peak of the spawning season, and that the larval census estimate has not been adjusted upward for the extrusion of larvae through the meshes of the plankton net. The scalor difference between the egg production and the larval census estimators probably results from inaccuracies in the coefficient of proportionality, 8.9×10^{-8}, of the larval census estimate (5) derived by Smith (1972).

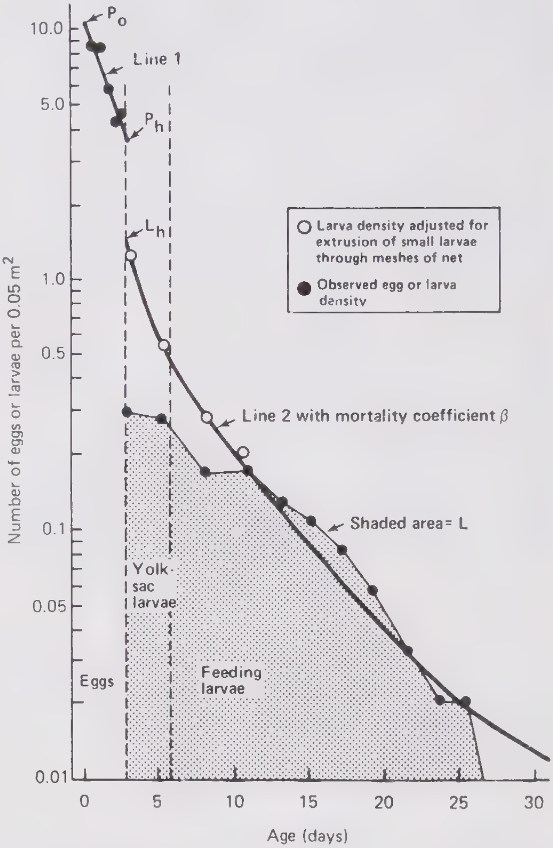

Figure 1. Conceptual basis for the calibration between the egg production and larval census estimators of anchovy spawning biomass. Lines 1 and 2 represent the mortality models for eggs and larvae, respectively.

CALIBRATION FOR AN EQUIVALENT LARVAL CENSUS ESTIMATE IN FUTURE YEARS

For years in which only an egg production survey is conducted, the optimum yield for the U.S. fishing season can be based on an equivalent larval census estimate of anchovy spawning biomass using the calibration equations (10) or (12). Estimates of egg parameters s, P' or p, and B_e can be derived from the egg production survey data. A weighted average of b for the surveys is 0.3835, given weights of ½ to the 1980 survey and ¼ to the two 1981 surveys. If a sufficient number of bongo plankton samples are collected during the egg production survey, a value of β can be estimated for the survey. Another alternative is to use the average value for 1980 and 1981 of 1.753.

A comparison of equivalent values versus the actual biomass estimates derived by larval census methods suggests that equations (10) or (12) overestimate the biomass by 3.1% using 0.3835 for b and yearly estimates of β. Procedures for estimating the precision of the predicting equations (10) or (12) have not been developed, primarily because of the unknown precision of the original biomass estimates for the larval census method.

ACKNOWLEDGMENTS

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☆ WEST PALM BEACH FL: Fish and their lives 8356

Tunas—Nomads of the Sea

by Michele Winkler, Shari E. Sitko
and Paul N. Sund

THE FISHERY for tunas is an ancient one, yet modern man does not know a great deal more about these fishes than his ancestors did. Their very nature poses a stumbling block, for tunas are the nomads of the seas.

The commercial tunas belong to the tribe Thunnini of the family Scombridae, and are related to such fishes as marlins, swordfish, and sailfish, whose speed, size, and stamina rank them among the world's most popular gamefishes. Because tunas are plentiful and occur in many geographic regions, they form the basis for some of the world's most thriving and productive commercial and recreational fisheries. Nearly 70 nations have coastal and inland tuna fisheries, using methods ranging from small primitive sailing boats to massive modern purse-seine liners. These fisheries are generally categorized according to depth fished or type of gear used. Pole-and-line, trolling, and netting purse-seine are used by the surface fisheries, while longliners fish the subsurface waters.

Different Species at Different Latitudes

The important commercial tunas fall into two major geographic groups: temperate and tropical. Temperate tunas inhabit both the northern and southern temperate latitudes. These include the northern and southern bluefin, and the albacore, which all

Albacore

migrate seasonally to warm-water regions for spawning.

The tropical tunas, which include the skipjack, yellowfin, and bigeye, are widely dispersed. Because they do not undertake a spawning migration, they tend to travel less and generally remain within the same geographic area throughout their lives.

The delicate-tasting tuna meat used in casseroles, salads, and other dishes usually comes from five major species. The mildly flavored canned white tuna sold in supermarkets is always albacore tuna. The somewhat darker, light-meat tuna which has a more pronounced flavor, comes from yellowfin, bigeye, bluefin, or skipjack.

Because tuna is nearly as costly as beef, most of the tunas harvested by other countries are exported as a cash crop. Ninety percent of the world's tuna catch is used in just a few countries: the United States, Japan, France, Spain, Italy, and West Germany.

Adult tunas encompass a wide size range. The tiny bullet tuna only reaches 7 pounds, while the giant bluefin can weigh 1,500 pounds or more. Their age can be determined by counting the rings that develop in the inner ear bones, or otoliths, in much the same way that a forester might count the growth rings on a tree. This research is still at an early stage, but results indicate that some species live from 15 to 20 years.

A Rarity — Warm-Blooded Fishes

Unlike almost all other fishes, tunas are thermoconserving, or warm-blooded, that is, they keep their bodies at temperatures higher than those of the surrounding waters. Scientists believe that the elevated temperature helps the tunas' eyes and brain to function more efficiently. This is particularly important because tunas locate their food primarily by sight, although smell may also be used. Their higher body temperature may also enable them to convert food more rapidly into energy, which they need for constant movement, respiration, and rapid bursts of swimming speed to pursue prey or escape predators.

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7 pounds = 3.17 Kilograms

1,500 pounds = 680 Kilograms

Yellowfin

Skipjack

Tunas are built for speed. They are among the fastest swimmers in the oceans and must move forward constantly to keep from sinking. They are very heavy in relation to their body length because of their densely packed muscles. They also lack or have a reduced swim bladder that would give them added buoyancy. The constant movement compensates for these physiological characteristics and also keeps a continuous passage of large volumes of water over the gills. This gives them the large supplies of oxygen they need for their metabolic processes.

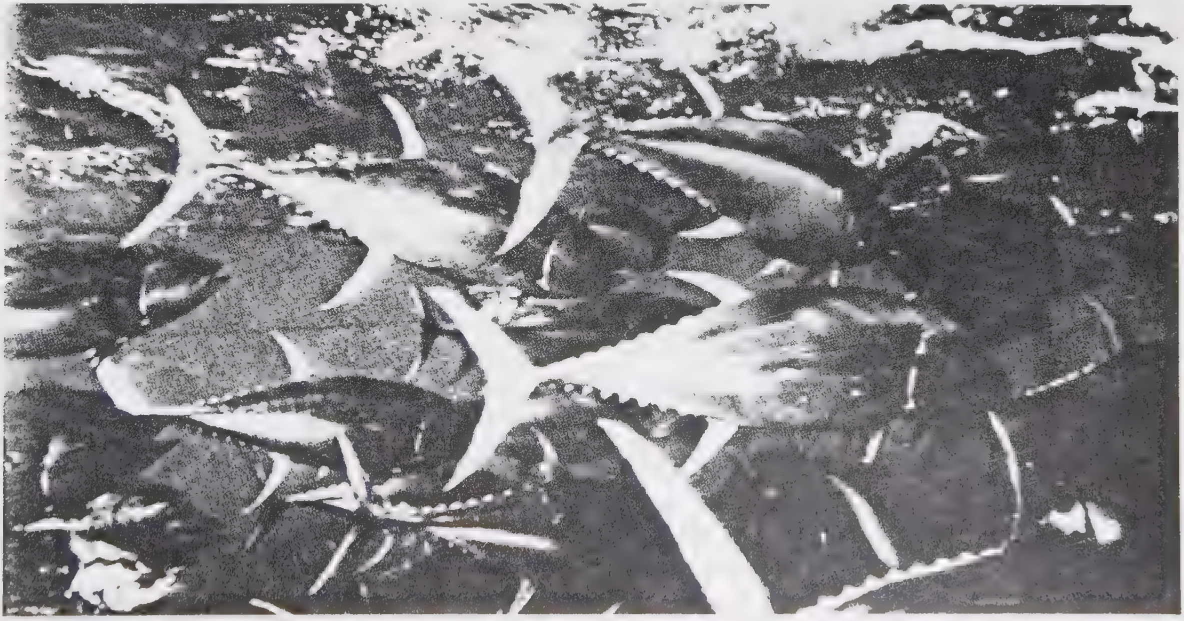
To fuel their bodies for this constant swimming, tunas require enormous amounts of food. A skipjack tuna can eat up to 25 percent of its weight each day, and 10 percent is common among other species. Small tunas (less than 15½ inches) can eat more than 30 percent of their body weight per day.

Tunas are opportunistic predators, eating whatever small moving prey they can catch. Although tunas have teeth, they usually gulp and swallow their prey whole. Smaller fishes, crustaceans, mollusks and, occasionally, plankton are all included in a typical tuna menu.

While stomach contents reveal what tunas feed upon, other aspects of their behavior such as mating practices are not well known. The parents do not appear to form a pair bond and do not provide care for the young. A male and female will separate from a school, release eggs and sperm into the water, and rejoin the group or swim off separately.

15½ inches = 39.4 centimeters

CLOSE BUT NEVER TOUCHING, *members of a yellowfin tuna school sense the presence of nearby individuals and keep their distance. Active, pelagic predators, tunas possess many adaptations for rapid swimming. Among them are a fusiform, torpedolike body which reduces drag, and a lunate or crescent-shaped tail which provides for the greatest forward thrust at a high hydrodynamic efficiency.*



In a single spawning, a female tuna releases many eggs, each about the size of a BB shot, and soft and rubbery in texture. Each egg contains an oil drop that causes it to float near the surface where it hatches after 30 hours. During its first few critical days of life, the larva lives off the yolk of its egg. After its digestive system has developed, the young tuna begins to hunt for food.

The chances of a larval tuna surviving its first few weeks of life are poor. Fighting to eat and not be eaten, only a few of the multitude of larvae will survive. Some will starve, but most will be eaten by other fishes, sea birds, and older tunas, which are cannibalistic. What little is known about the life stages of tunas under 12 inches has been learned from studying the stomach contents of larger fishes.

Schools Only for the Young

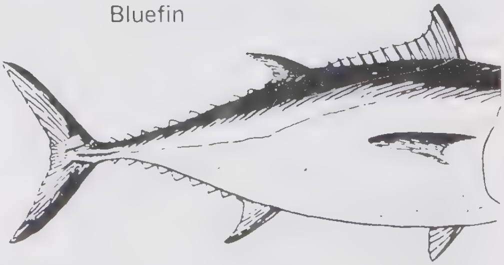
It is known that young tunas grow quickly and remain near the surface of the ocean for their first three or four years. The survivors of a single spawning often swim and feed together in schools. Some of these schools may contain several species of young tunas, for the young generally prefer the warmer surface waters while the adults seek the cooler temperatures of the depths. This schooling behavior may protect the young because the constantly shifting and shimmering mass of the school makes it difficult for a predator to single out an individual to attack.

These surface schools are important to fishermen because enough tunas aggregate to make fishing profitable. In order to effectively manage these valuable tuna resources, however, scientists must define the areas occupied by these composite or

SMALL AND DELICATE, *juvenile yellowfin tuna must be handled with forceps. They grow rapidly, reaching an average weight of 7 pounds by the end of their first year and as adults may weigh up to 350 pounds.*

All illustrations courtesy of National Marine Fisheries Service except where otherwise noted

Bluefin



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12 inches = 30.5 centimeters

mixed schools, determine how and where the fishes move seasonally, and observe how members of each species in the schools mingle with tunas from other areas.

A tuna remains in surface schools for about five years. Then, for reasons scientists have yet to discover, it abandons the schools and becomes a more solitary, deepwater swimmer. Information concerning the swimming depths of the important commercial tunas has primarily come from depth measurements taken during fishing operations and research fishing tests. It has been found that the species composition will vary according to the season and geographic area being fished and the vertical distribution of the tunas. Different tuna species have different tolerances to ocean temperatures and oxygen levels. These tolerances will help stratify the tunas within a given area, not only by species but also by age group within a species.

In the early 1970s, the Japanese, who support a large tuna fishing industry, experimented with special vertical long-line fishing gear in order to record accurately depth information for commercially important species of tuna. Japanese scientists, Drs. S. Saito and S. Sasaki, designed equipment that had a depth recorder attached at each hook on a long-line. These scientists tested their gear west of Fiji. There they found that yellowfin and albacore tunas were abundant above 1,000 feet, but catches of these tunas declined rapidly below that point. However, the bigeye tuna, a premium, high-quality tuna important to the world's fisheries and the Japanese market in particular, appeared much more frequently below 1,000 feet, with its abundance still increasing at 1,246 feet, the deepest level fished in these experiments.

Reaching Deeper for Bigeye

The long-line gear currently in use can reach to 1,000 feet. While this will catch most species of commercial tunas, Saito and Sasaki believe that it does not reach the most abundant depths for bigeye tuna. The Japanese are now modifying their long-line

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1,000 feet = 305 meters; 1,246 feet = 380 meters

Bigeye

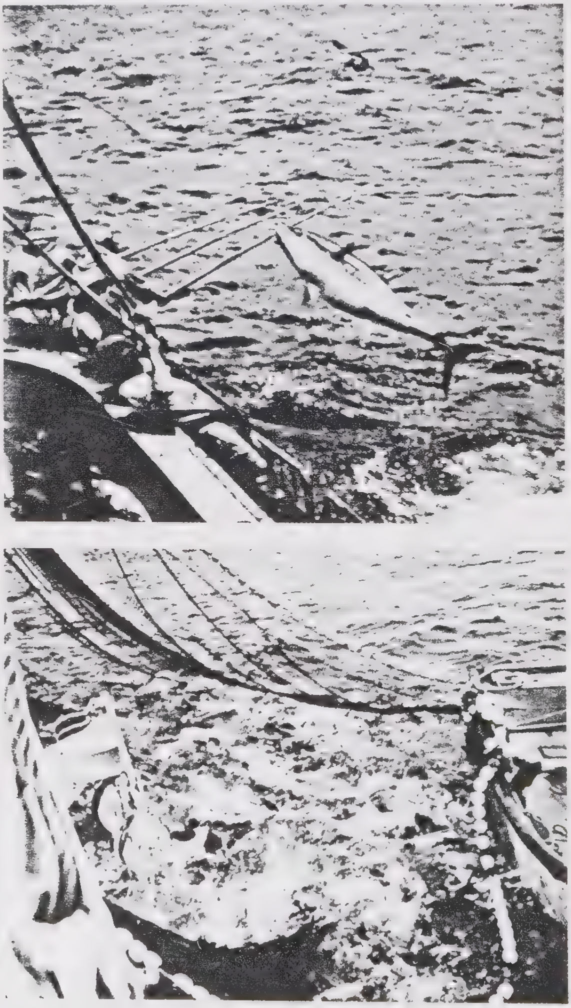
gear in order to fish for this valuable species at a greater, and possibly more profitable, depth.

Tunas have the ability to migrate large distances, covering from 9 to 31 miles per day, and they can move independently of the ocean's currents. However, each species has limits on its distribution which keep it from ranging throughout all oceans.

One way to gather information on the movement of tunas is by tagging a fish and releasing it for recapture at a later date. When the fish is recaptured and the tag returned, the scientist can tell how far the fish has traveled between the two capture times. This will be a minimum distance traveled, since the fish will not always move in a straight line from one point to another. In addition to the time and place of capture, information concerning length and weight, fat content, blood, and general condition of the fish can be compared from the time that the fish was tagged to the time of its recapture.

There is some disagreement among scientists as to whether tunas undertake migrations or whether they simply travel along with the prevailing currents. Perhaps continuing studies will some day shed more light on the movements and life style of these magnificent wanderers — these nomads of the sea. □

Taking a flying leap, *a yellowfin tuna is hooked by a pole-and-line fisherman (upper). Purse-seining which accounts for 30 percent of the world tuna catch utilizes nets (lower) sometimes over ½ mile long to encircle schools of tuna.*



Bottom: Inter American Tropical Tuna Commission

Yellowfin

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9 to 31 miles = 14 to 50 kilometers

8357

ЗООЛОГИЧЕСКИЙ ЖУРНАЛ

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ОЦЕНКА ФЕНЕТИЧЕСКИХ ОТНОШЕНИЙ ГРУППИРОВОК ДЕЛЬФИНОВ НА ОСНОВЕ АНАЛИЗА НЕМЕТРИЧЕСКИХ ВАРИАЦИЙ ЧЕРЕПА

А. В. ЯБЛОКОВ, У. Ф. ПЕРРИН, М. В. МИНА

Исследованы неметрические вариации 31 признака в пяти выборках (185 черепов) *Stenella attenuata* и в двух выборках (34 черепа) *S. longirostris*, взятых в Тихом океане у берегов южной Мексики и Центральной Америки. Выборки сравнивали по 15 признакам, вариации которых не обнаруживали зависимости от пола и возраста особей. Обобщенная оценка фенетического сходства выборок была произведена с помощью «индекса сходства», предложенного Животовским (1982). Выборки *S. attenuata*, взятые вдали от берегов, объединяются и обособляются от «прибрежной» выборки. Выборки *S. longirostris* отличаются друг от друга больше, чем какие-либо две выборки *S. attenuata*. Обсуждается дискриминативная ценность признаков.

За последние два десятилетия в популяционной биологии получил развитие анализ дискретных, в большинстве своем — неметрических признаков, проводимый для того, чтобы непосредственно оценить фенетические (а опосредованно-генетические) отношения между внутривидовыми группировками животных. Изучение неметрических вариаций черепа у ряда видов грызунов, приматов, хищных и ластоногих показало, что многие признаки этой категории могут использоваться как маркеры генотипического состава популяций, благодаря чему становятся возможными выделение совокупностей генетически сходных особей и анализ взаимоотношений этих совокупностей (Berry, Searle, 1963; Berry, 1977; Sjøvold, 1977; Hartman, 1980; Ларина, Еремина, 1982; Большаков, Васильев, 1975 и др.; обзор см. Яблоков, 1980). Делались попытки использовать в тех же целях неметрические вариации посткраниального скелета китообразных (Белькович, Яблоков, 1965; Berzin, Veinger, 1982).

Благодаря тому, что с 1968 г. сотрудниками Юго-западного рыбохозяйственного центра США собирается коллекция черепов дельфинов рода *Stenella* (*S. attenuata*, *S. longirostris*), погибающих при промысле тунцов в Тихом океане (Perrin, 1969), возникла возможность изучить в популяционно-морфологическом аспекте неметрические вариации черепа китообразных на достаточно большом материале.

В задачи нашей работы входило выявление неметрических вариаций черепа *S. attenuata* и *S. longirostris*, разработка методики анализа этих вариаций, оценка зависимости признаков от возраста и пола особей, выяснение фенетических отношений пространственно разобщенных группировок особей одного вида и разных видов, а также сравнение полученных результатов с результатами изучения изменчивости этих видов по иным признакам (Perrin, 1975 a).

Материал, использованный в настоящем исследовании, включал черепа 185 экз. *S. attenuata* (5 выборок) и 34 экз. *S. longirostris* (2 выборки), погибших во время промысла тунцов в водах Южной Мексики и Центральной Америки (рис. 1). Бо́льшая часть этого материала хранится в Национальном музее естественной истории США

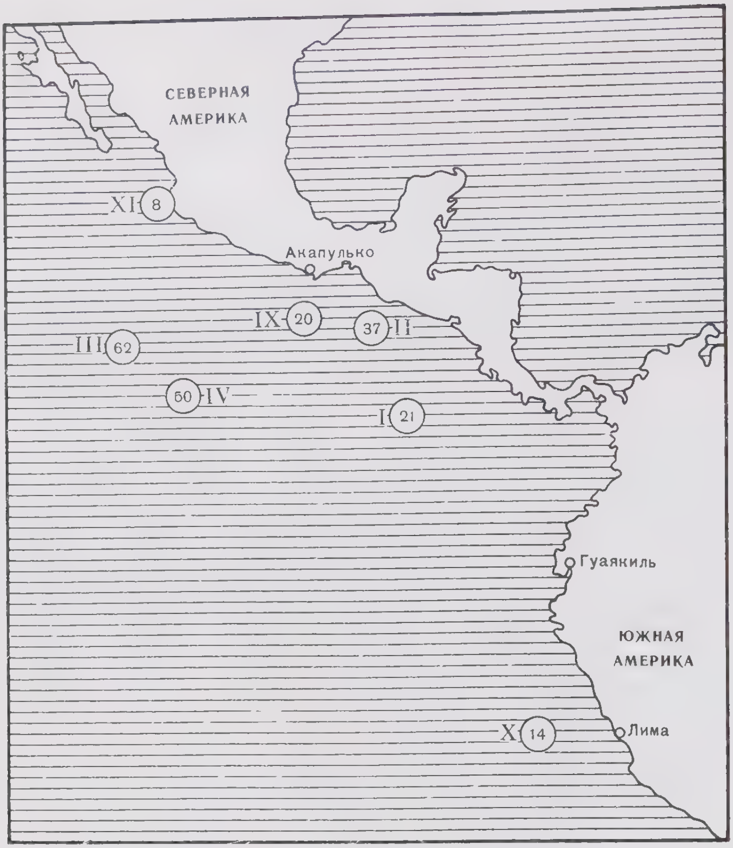

Рис. 1. Места взятия исследованных выборок *Stenella attenuata* и *S. longirostris* (по Perrin et al., 1982): римские цифры — номера выборок, арабские — число особей в выборках

(Вашингтон), меньшая — в Музее естественной истории в г. Сан-Диего и Юго-западном рыбохозяйственном центре США (Калифорния).

На первом этапе работы были выделены неметрические вариации черепа, подобные тем, которые выделялись исследователями, имевшими дело с млекопитающими других отрядов (Berry, Searle, 1963; Berry, 1963, 1969; Hilborn, 1974; Рычков, Мовсесян, 1972; Турутина, 1982 и др.). Выяснилось, что для ряда признаков не удается выработать систему оценки по двум состояниям («есть — нет»). Использование в фенетическом анализе признаков, одни из которых могут быть описаны по двум, а другие — по большему числу состояний (вариантов), сопряжено с определенными методическими трудностями (Sjøvold, 1977). Преодолеть эти трудности можно с помощью показателя сходства, предложенного Животовским (1979, 1980, 1982). Если в одной из сравниваемых выборок частоты (доли) конкретных вариантов (состояний) признака составляют $p_1, p_2 \dots p_m$, а в другой соответственно $q_1, q_2 \dots q_m$, то показатель сходства $r = \sum_{i=1}^{m} \sqrt{p_i \cdot q_i}$. Достоверность различий оценивается с помощью критерия идентичности

$$I = [8N_1N_2/(N_1+N_2)] \cdot [1 - r - (p^0+q^0)/4],$$

где N_1 и N_2 — число особей в сравниваемых выборках, p^0 — сумма частот состояний, представленных в первой выборке и не представленных во второй, q^0 — сумма частот состояний, представленных во второй выборке и не представленных в первой. Величина I распределена как χ^2 с $m-1$ степенями свободы.

При анализе n статистически независимых признаков среднее сходство оценивается величиной $\bar{r} = 1/n(r_1+r_2+\dots+r_n)$, для которой $I = I_1+I_2+\dots+I_n$ (число степеней свободы $df = m_1+m_2+m_3+\dots m_n-n$).

Для каждого предварительно выделенного признака два первых автора настоящей статьи оценивали возможность установления однозначного соответствия каждого экземпляра определенному состоянию данного признака. Если установить такое соответствие не удавалось, признак исключался из дальнейшего рассмотрения. Детальному анализу в дальнейшем подвергались только те признаки, которые могли быть охарактеризованы по всем имевшимся выборкам. В связи с этим, в частности, из рассмотрения были исключены все неметрические вариации нижней челюсти и зубного ряда верхней челюсти. В результате общее число признаков, подлежащих рассмотрению в сравнительном аспекте, составило 31. В случае билатерального расположения структур для настоящего анализа были взяты признаки левой стороны черепа. Полное описание всех выделенных признаков, а также полные данные по возрастному и половому составу отдельных выборок были опубликованы ранее (Perrin et al., 1982).

ОПИСАНИЕ ПРИЗНАКОВ

1. Положение отверстий для средней ветви внутриглазничного нерва (foramen infraorbitale mediale) по отношению к уровню переднего края предглазничных отростков: на уровне линии «*a*» (рис. 2, *A*), впереди или позади.

2. Положение отверстий для боковой ветви внутриглазничного нерва (for. infraorbitale laterale) по отношению к уровню переднего края предглазничных отростков: на уровне линии «*a*» (рис. 2, *A*), впереди или позади.

3. Взаиморасположение правого и левого отверстий для боковых ветвей внутриглазничного нерва: на одном уровне по отношению к продольной оси черепа, левое впереди, правое впереди.

4. Положение канала отверстия боковой ветви внутриглазничного нерва: зондируется (не зондируется) вертикально.

5. Число (0—5) отверстий для ростральных ветвей верхнечелюстного нерва (for. maxillare superius) кпереди от отверстия боковой ветви внутриглазничного нерва.

6. Число (0—3) отверстий для ветвей лицевой артерии, идущих вместе с конечными ветвями глазничного нерва (for. supraorbitale) и верхнечелюстного нерва (for. zygomatico-faciale) позади переднего края костной ноздри (линия «*b*» на рис. 2, *A*).

7. Число и положение вырезок на os praemaxillare в переднем крае костной ноздри, через которые видна os maxillare: 1) нет вырезок; 2) вырезка, выходящая одновременно на медиальный и аборальный края os praemaxillare; 3) вырезка только на медиальном крае (рис. 2, *A*, *fen*); 4) округлая вырезка, не выходящая на края кости (рис. 2, *A*, *fen*); 5) комбинация вариантов 2 и 3; 6) вырезка на аборальном крае вместе с вариантом 2; 7) комбинация вариантов 2 и 4.

8. Развитие гребня (crista mesethmoidalis) у переднего края костной ноздри: гребень доходит (или почти доходит) до дорсальной поверхности os praemaxillare или заметно ниже этого уровня.

9. Наличие (отсутствие) соприкосновения os maxillare и os occipitale в точке, где затылочный гребень пересекает височную яму (рис. 2, *A*, *c*). Отсутствие соприкосновения фиксируется, если расстояние между костями в этой точке более 1 мм.

10. Наличие (отсутствие) соприкосновения между os praemaxillare и os nasale (рис. 2, *A*, *d*). Отсутствие соприкосновения фиксируется, если расстояние между костями более 1 мм.

11. Левый край наружной костной ноздри на уровне окончания os praemaxillare (рис. 2, *A*, *e*) при взгляде сверху формируется: только os praemaxillare или os maxillare и os praemaxillare.

12. Присутствие (отсутствие) переднеорбитальной вырезки (рис. 2, *A*, *f*).

13. Нижний край скулового отростка (processus orbitalis anterior) при взгляде сбоку формируется: только os lacrimale; os lacrimale и os frontale; os lacrimale и os maxillare.

15. Затылочный гребень (protuberantia occipitalis medialis) (рис. 2, *Б*, *p. o. m*) на уровне середины затылочных бугров при проверке краем

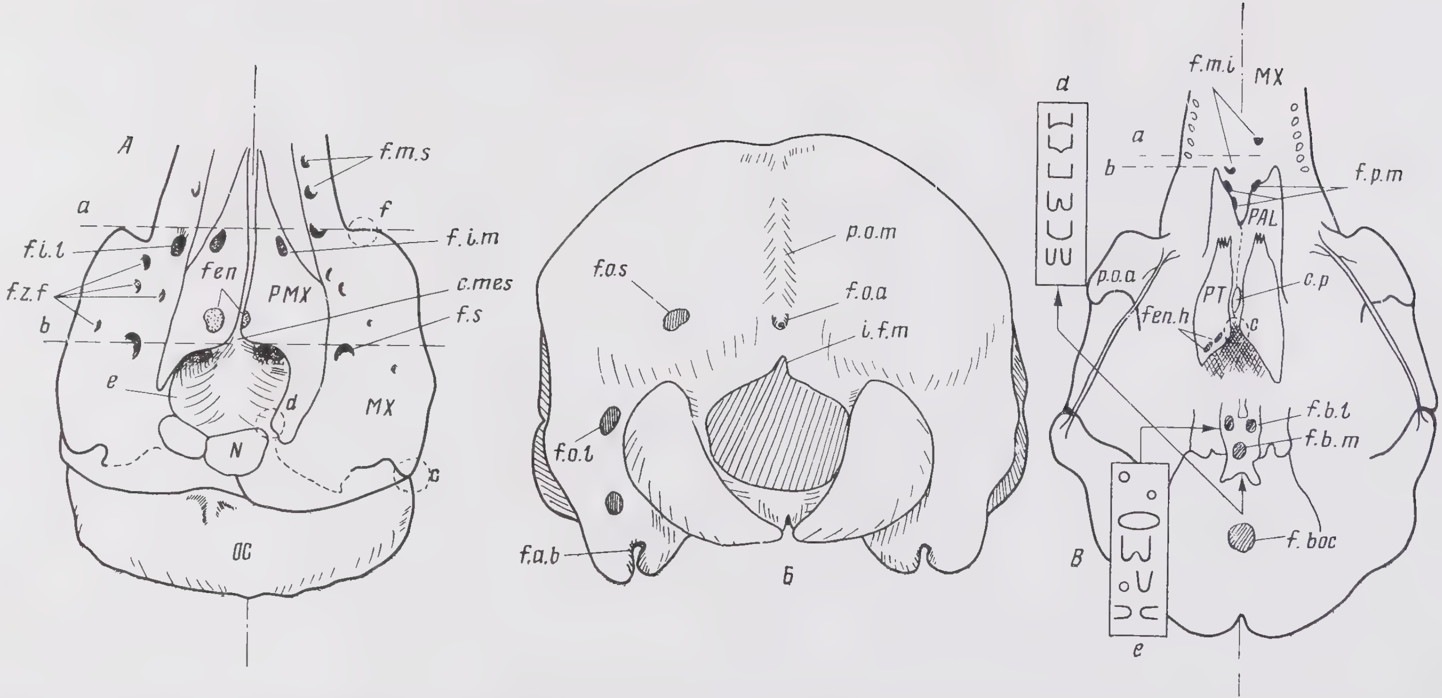

Рис. 2. Схема расположения основных изученных признаков на дорсальной (*А*), затылочной (*Б*) и вентральной (*В*) поверхности черепа (на правой и левой половинах черепа показаны разные варианты отдельных признаков): *MX* — os maxillare, *N* — os nasale, *OC* — os occipitale, *PAL* — os palatinum, *PMX* — os praemaxillare, *PT* — os pterygoideum (hamulus), *c. mes* — crista mesethmoidalis, *c. p* — crista palatina, *fen* — fenestrae praemaxillares, *fen. h* — fenestrae hamuli pterygoidei aboralis, *f. b. l* — fen. basisphenoidalis lateralis, *f. b. m* — fen. basisphenoidalis medialis, *f. boc* — fen. basioccipitalis, *f. p. m* — for. palatina majora, *f. m. i* — for. maxillaria interna, *f. o. a* — for. occipitale-accessorium, *f. a. b* — for. arteriale basilare, *f. o. l* — fen. occipitalis lateralis, *f. o. s* — fen. occipitalis superior, *f. i. l* — foramen infraorbitale laterale, *f. i. m* — for. infraorbitale mediale, *f. m. s* — for maxillare superius, *f. s* — for. supraorbitale, *f. z. f* — for. zygomatico-faciale, *i. f. m* — incisura foraminis magni, *p. o. a* — proc. orbitalis anterior, *p. o. m* — protuberantia occipitalis medialis; *a*—*f* — см. описание признаков в тексте

линейки достигает (или превышает) этот уровень или не достигает этого уровня.

16. Наличие (отсутствие) дополнительного затылочного отверстия (*for. occipitale accessorium*) над большим затылочным отверстием (рис. 2, *Б, f. o. a*).

17. Наличие (отсутствие) вертикальной вырезки на дорсальной стороне затылочного отверстия (рис. 2, *Б, i. f. m*).

18. Число (0—3) прободений затылочной кости латерально от мыщелка (рис. 2, *Б, f. o. l*).

19. Число (0—2) прободений затылочной кости в районе затылочного бугра (рис. 2, *Б, f. o. s*).

20. Положение конца зубного ряда (центра последнего зуба или последней альвеолы) с каждой стороны по отношению к переднему краю os palatinum: на уровне, впереди или позади (рис. 2, *В, a*).

21. Расположение отверстий для внутренних ветвей верхнечелюстного нерва (for. maxillaria interna) с каждой стороны: на уровне переднего края os palatinum, впереди или позади этого уровня (рис. 2, *В, f. m. i, b*).

22. Число крупных (более 1 мм диаметром) отверстий для ветвей верхнечелюстного нерва (for. palatina majora) на границе между os maxillare и os palatinum с каждой стороны.

23. Наличие (отсутствие) контакта между отростками крыловидной кости (hamuli pterygoidei) у переднего края хоан (рис. 2, *В, c*). Отсутствием контакта считается положение костей на расстоянии более 1 мм.

24. Наличие (отсутствие) соединения отростков крыловидной кости в передней их части. Отсутствием соединения считается положение костей на расстоянии более 1 мм.

25. Присутствие (отсутствие) гребня небной кости (crista palatina) в пространстве между отростками крыловидных костей (рис. 2, *В, c. p*).

26. Форма задней части отростков крыловидных костей: удлиненная (ширина основания отростка меньше его длины, рис. 2, *В, pt*, справа) или укороченная (рис. 2, *В, pt*, слева).

27. Присутствие (отсутствие) прободений в задней части hamuli pterygoidei (рис. 2, *В, fen. h*).

28. Форма заднего края os basisphenoidale (6 вариантов, см. рис. 2, *В, d*).

29. Форма и положение боковых отверстий на os basisphenoidale (8 вариантов, см. рис. 2, *В, e*).

30. Присутствие (отсутствие) центрального отверстия (fen. basisphenoidalis medialis) на os basisphenoidale (рис. 2, *В, f. b. m*).

31. Характер прободения os basioccipitale: от 0 до 3 отверстий в разных сочетаниях (рис. 2, *В, f. boc*).

32. Наличие (отсутствие) видимого при взгляде сзади — снизу for. arteriale basilare в яремной щели (рис. 2, *Б, f. a. b*).

АНАЛИЗ ЗАВИСИМОСТИ ПРИЗНАКОВ ОТ ПОЛА И ВОЗРАСТА ОСОБЕЙ

Используя выборку IV *S. attenuata*, включающую наибольшее число взрослых особей, мы сравнили по каждому признаку взрослых самцов ($n=16$) и взрослых самок ($n=12$). В тех случаях, когда достоверность различий, определенная по критерию *I*, оказалась ниже порогового значения ($\chi^2_{0,05}$), провели сравнение взрослых особей (самцов и самок вкупе) с неполовозрелыми[1] ($n=22$).

Достоверные различия между самцами и самками были обнаружены по двум признакам (23 и 32). По одному признаку (11) такие различия были выявлены между неполовозрелыми самцами и самками.

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[1] Разделение особей на половозрелых и неполовозрелых проводилось по степени слияния maxillae и praemaxillae на роструме (Perrin, 1975).

Достоверные различия между взрослыми и неполовозрелыми особями были найдены по 11 признакам (1, 7, 9, 12, 19, 20, 22, 27, 28, 29, 31).

Зависимость признаков от пола и возраста особей у *S. longirostris* характеризовали, объединив выборки IX и X, благодаря чему сравниваемые группы включали 17 (взрослые самцы), 12 (взрослые самки) и 6 экз. (неполовозрелые особи). Анализировались только те признаки, для которых не было найдено зависимости от пола и возраста у *S. attenuata.* Достоверные различия между взрослыми самцами и самками были обнаружены по признаку 6, а между взрослыми и неполовозрелыми особями — по признаку 13.

Таким образом, пригодными для сравнения выборок, представляющих пространственно разобщенные группировки (стада) дельфинов, оказались 15 признаков.

СРАВНЕНИЕ ПРОСТРАНСТВЕННО РАЗОБЩЕННЫХ ВЫБОРОК

На основании оценок сходства между выборками *S. attenuata*, приведенных в таблице, выборки I, II, III и IV объединяются в компактную группу и от них отделяется выборка XI (рис. 3). Две имеющиеся выборки *S. longirostris* (IX и X) обнаруживают между собой меньшее сходство, чем любые две выборки *S. attenuata* (таблица). Во всех попарных сопоставлениях различия между выборками по совокупности 15 признаков достоверны, причем в сопоставлениях выборок I и II с выборкой XI $0{,}01 < p < 0{,}05$, в остальных же случаях $p < 0{,}01$.

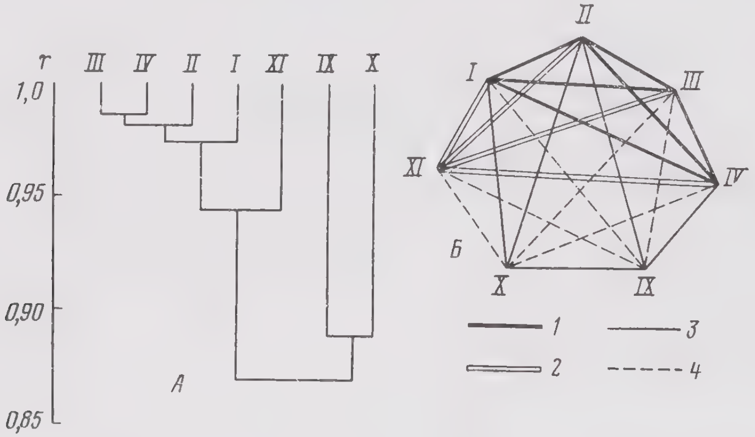

Рис. 3. Дендрограмма, построенная односвязным методом (*А*), и граф (*Б*), представляющие фенетические отношения изученных выборок: *1* — $\bar{r}$ от 0,96 до 1,00; *2* — $\bar{r}$ от 0,91 до 0,95; *3* — $\bar{r}$ от 0,86 до 0,90; *4* — $\bar{r}$ от 0,81 до 0,85; римскими цифрами обозначены выборки

В целом можно констатировать большое сходство по исследованному набору признаков между *S. attenuata* и *S. longirostris*, причем группа выборок I—IV фенетически ближе к *S. longirostris*, чем выборка XI (таблица, рис. 3).

Приведенные выше данные свидетельствуют, что мелкие неметрические вариации, затрагивающие в основном форму отдельных деталей различных костей лицевого и мозгового черепа, присутствие и расположение отверстий для нервов и кровеносных сосудов, а также врожденных прободений отдельных костей (в основном мозгового черепа), обычные в черепе грызунов, приматов, хищных и ластоногих, встречаются и

*Усредненные оценки сходства ($\bar{r}$) и значения критерия идентичности (I) для выборок Stenella attenuata и S. longirostris по 15 неметрическим признакам черепа**

Выборки	I	II	III	IV	IX	X	XI
I		0,971	0,974	0,975	0,845	0,856	0,943
II	$\frac{42,91}{21}$		0,977	0,982	0,870	0,865	0,940
III	$\frac{35,32}{21}$	$\frac{51,22}{23}$		0,984	0,850	0,842	0,939
IV	$\frac{41,98}{21}$	$\frac{50,86}{21}$	$\frac{78,34}{23}$		0,858	0,855	0,931
IX	$\frac{176,47}{20}$	$\frac{152,59}{22}$	$\frac{224,91}{23}$	$\frac{205,25}{22}$		0,890	0,815
X	$\frac{128,75}{20}$	$\frac{141,32}{21}$	$\frac{138,45}{22}$	$\frac{165,84}{21}$	$\frac{100,30}{20}$		0,846
XI	$\frac{32,01}{19}$	$\frac{38,38}{21}$	$\frac{40,22}{19}$	$\frac{49,86}{21}$	$\frac{95,15}{20}$	$\frac{58,69}{19}$	

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* Выше диагонали — оценки $\bar{r}$, ниже диагонали для каждого сравнения над чертой — значения I, под чертой — число степеней свободы.

в черепе китообразных и, по всей вероятности, могут характеризовать своими частотами встречаемости определенные естественные группировки особей.

В то же время проведенный анализ показал, что при использовании неметрических вариаций черепа для оценки фенетических отношений отдельных сравниваемых групп дельфинов необходимо учитывать возможную зависимость таких признаков от возраста, а некоторых — также и от пола особей.

Полученные результаты позволяют говорить о большей обособленности прибрежной группировки *S. attenuata* от группировок открытого океана в сравнении с обособленностью отдельных групп (стад) дельфинов открытого океана друг от друга. Более того, можно предположить, что стада дельфинов открытого океана, представленные в нашем материале, не являются длительно существующими, изолированными, самовоспроизводящимися группировками — отдельными популяциями в генетико-эволюционном смысле слова.

Уровень фенетического (и предположительно — генетического) сходства стад *S. longirostris*, обитающих к северу и к югу от экватора, таков, что возникают основания для вывода об их значительной генетической разобщенности. Во всяком случае, величина различий между ними превышает уровень различий прибрежных и «океанических» групп *S. attenuata*.

Все данные о сходстве и различиях между группировками, полученные при анализе неметрических вариаций черепа исследованных видов дельфинов, полностью совпадают с результатами, полученными при сравнении размеров и пропорций черепа, а также особенностей окраски особей этих групп (Perrin, 1975, 1975a). Это обстоятельство может рассматриваться как подтверждение возможности использования фенетических дистанций для объективного изучения структуры внутривидовой изменчивости китообразных.

Примененный метод анализа полученных данных, к сожалению, не позволил выделить родственные группы особей (типа семейных группировок) внутри отдельных стад. Что такие группировки могут быть выявлены, предположил один из авторов настоящей статьи (А. В. Яблоков) при визуальном анализе коллекционного материала на основании значительного сходства между некоторыми животными по характеру мелких вариаций. В дальнейшем было бы интересно проанализировать как имеющийся, так и дополнительный материал по неметрическим вариациям в черепе китообразных со специальной целью поиска признаков, могущих показать сходство (родство) отдельных особей.

Проведенный анализ неметрических признаков позволяет сделать некоторые общие замечания, касающиеся дальнейшего развития фенетического подхода при анализе внутри- и межвидовой изменчивости. Исследованные нами признаки имеют заведомо разную «дискриминативную» ценность, в разной мере выявляя различия между сравниваемыми группами особей. Это подтверждает представление о различном «фенетическом масштабе» разных признаков (Яблоков, 1980).

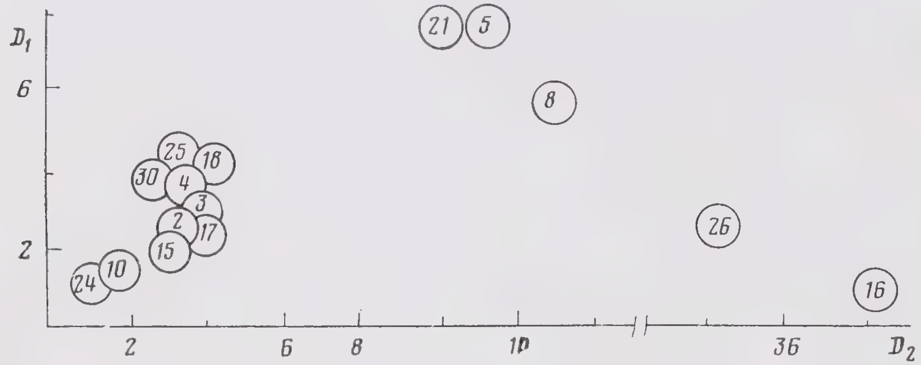

Рис. 4. Соотношение значений D, характеризующих дискриминативную ценность признаков: D_1 — в группе выборок *S. attenuata*, D_2 — в группе выборок *S. attenuata* и *S. longirostris*

$$D = 100 \cdot \sqrt{\frac{\Sigma (\bar{r} - r_i)^2}{n - 1}}$$

Выбор признаков, наиболее ценных для решения задач конкретного исследования, представляется важнейшей проблемой, успех решения которой может определить перспективы использования неметрических вариаций в целом. Мы пытались в первом приближении оценить дискриминативную ценность признаков величиной дисперсии значений r, полученных в попарных сравнениях выборок данного множества. Такие оценки были вычислены для всех семи выборок обоих видов и отдельно — для пяти выборок *S. attenuata*. Как и следовало ожидать, при анализе разных по составу групп выборок наиболее ценными оказываются разные признаки (рис. 4). Выясняется также, что дискриминативная ценность признаков сильно варьирует. Из этих результатов следуют, по крайней мере, два вывода. Во-первых, при описании фенетических отношений внутривидовых группировок у разных видов (даже весьма близких друг другу) нельзя заранее быть уверенным, что признаки, хорошо дифференцирующие группировки одного вида, будут столь же хорошо дифференцировать группировки другого. Во-вторых, поскольку использованные нами признаки были выбраны без предварительной оценки их дискриминативной ценности, логично предполагать, что в будущем, получив такую оценку, удастся в каждом случае выделять набор неметрических признаков, более четко характеризующих фенетические отношения исследуемых группировок.

Подводя итог проделанной работе, прежде всего подчеркнем, что интересным представляется сам факт обнаружения таких неметрических вариаций черепа китообразных, которые могут быть подвергнуты популяционно-морфологическому анализу.

Для обработки имеющегося и сравнительно немногочисленного пока по числу исследованных особей и отдельных выборок материала по неметрическим вариациям в черепе китообразных простым и вместе с тем достаточно эффективным методом оценки степени сходства по полиморфным признакам оказался метод, предложенный Л. А. Животовским. Мы предполагаем, что этот метод может быть широко использован для решения популяционно-морфологических задач на аналогичном материале и по другим группам животных.

В настоящее время трудно оценить перспективы использования неметрических вариаций черепа для выявления фенетических (и генетических) отношений видов и внутривидовых группировок китообразных вообще и дельфинов в частности. Однако приведенные выше результаты позволяют считать, что этот подход может быть, по меньшей мере, ценным дополнением к обычно применяемому для этих целей анализу пластических, меристических и других количественных признаков.

Настоящее исследование было проведено в рамках проекта «Морские млекопитающие» Межправительственного соглашения СССР — США по охране окружающей среды 1972 г. Мы благодарны В. А. Земскому, Ю. Е. Казакову, С. Г. Колю, Р. В. Миллеру, Л. А. Попову, В. Сильвермен, В. И. С пакову и другим, кто обеспечивал успешную работу этого проекта. Мы признательны также Дж. М. Кое, В. Оливер, Б. Г. Барго и Д. Дж. Трюдо, собравшим бо́льшую часть исследованных материалов, а также владельцам, капитанам и командам сейнеров «Carol Virginia», «Eastern Pacific», «Independence» «King Oscar», «Lois Seaver», без содействия которых сбор материала был бы невозможен. Наконец, мы благодарны Дж. Г. Миду (Национальный музей естественной истории, Вашингтон) и А. Реа (Музей естественной истории, Сан-Диего) за большую помощь в работе над коллекционным материалом.

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Институт биологии развития АН СССР (Москва),
Юго-западный центр рыбохозяйственных
исследований США (Ла-Холья, Калифорния)

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EVALUATION OF PHENETIC RELATIONS AMONG GROUPS OF DOLPHINS USING ANALYSIS OF NON-METRIC CRANIAL VARIATION

A. V. YABLOKOV, W. F. PERRIN, M. V. MINA

Institute of Developmental Biology, USSR Academy of Sciences (Moscow)
and Southwest Fisheries Center (La Jolla, California, USA)

Summary

Non-metric variation of 31 characters was studied in 5 samples (185 skulls) of *Stenella attenuata* and in 2 samples (34 skulls) of *S. longirostris* from off the Pacific coasts of southern Mexico and Central America. The samples were compared using 15 characters found to be independent of sex and age. An integrative «index of similarity» (Zhivotovskiy, 1982) was calculated. Offshore samples of *S. attenuata* showed a high degree of similarity and differed sharply from a coastal sample. The two samples of *S. longirostris* differed more from each other than did any two of the samples of *S. attenuata*. The discriminative power of the characters is discussed.

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